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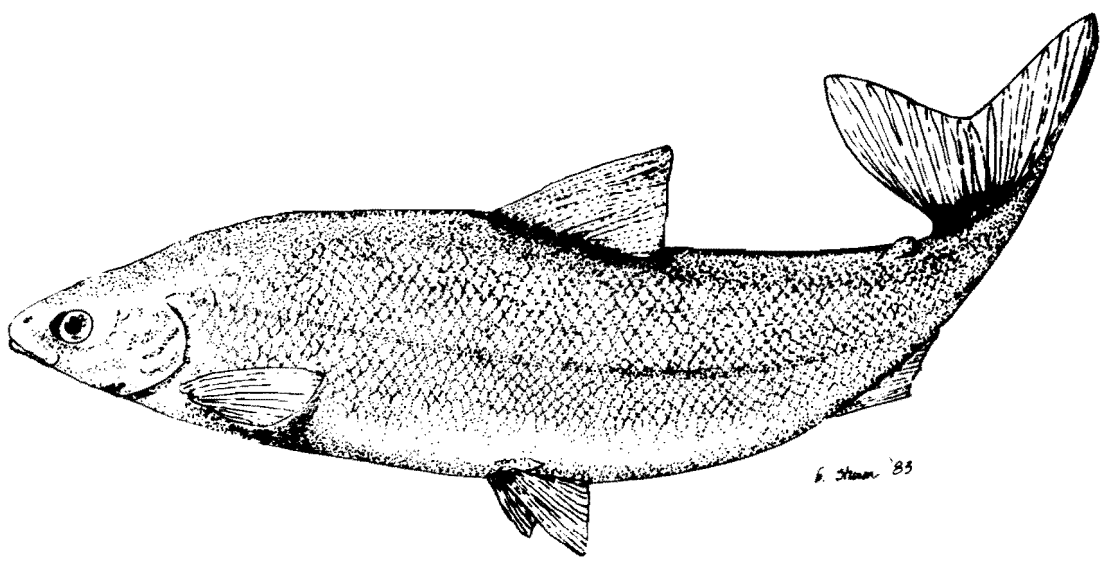
Nine papers contributing to an ecological synthesis

Edited by David W. Norton



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RESEARCH ADVANCES ON ANADROMOUS FISH IN ARCTIC ALASKA AND CANADA

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Research Advances on Anadromous Fish in Arctic Alaska and Canada

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Editor's Introduction

Any reader confronting this sizable volume of papers devoted to arctic anadromous fish deserves some explanation of the genesis of this collection. For this background, it may help to understand why so many resources have been expended on the general topic since the early 1970s. The welfare of anadromous fish populations in the nearshore waters of the US and Canadian Beaufort Sea has been a dominant regional theme of environmental investigations linked to petroleum development over this period. The investment in these investigations reached between $20 and $25 million by late 1988. Such an investment clearly dwarfs the commercial value of the fishery, which is largely characterized as subsistence, domestic, or personal-use. Important as these resources are to coastal residents from Point Hope to Cape Dalhousie, the scale of concern and investment in ecological investigations would seem (from a global perspective) more appropriate for the maricultural resources in the Sea of Japan or the international fisheries of the southern Bering Sea.

This disproportionate investment is historically rooted in the position maintained among scientists representing several resource agencies. This position holds that continuous-fill causeways projecting into the nearshore marine environment represent serious and unnecessary threats to the coastal ecosystems and to the fishes that inhabit them. The single event that focused this concern can be traced to the autumn of 1975. Sea ice that year was unusually heavy and persistent. The annual sealift of heavy equipment and modular buildings for the Prudhoe Bay oilfield became trapped in nearshore sea ice some 2,000 metres seaward of the end of the existing Prudhoe Bay Causeway, or "West Dock." Construction of the Trans-Alaska Pipeline was then nearing 50 percent completion. Prompt landing of the cargo of the 1975 sealift was deemed critical by the petroleum industry to meet tight construction schedules for the start of oil delivery from the Prudhoe Bay field by 1977. The solution proposed by industry for landing this cargo was to extend the existing causeway by continuing it as a solid-fill gravel structure, out to the point where sealift barges were stuck. Opponents of this emergency solution contended that an extended solid-fill causeway was an unnecessary, permanent barrier to the migration of anadromous fishes in the coastal longshore plume of relatively warm and low-salinity waters. The alternative solution proposed by these opponents was to thicken the sea ice between West Dock and the trapped sealift fleet so that the cargo could be driven over a solid and grounded but temporary ice road.

The gravel-fill causeway extension plan prevailed. Ever since that episode, the concern for anadromous fish populations has been an institutionalized ingredient in each of the subsequent planned coastal modifications in support of petroleum developments in arctic Alaska and Canada. In turn, field investigations of anadromous fish ecology have been mandated and carried out annually for each significant project that might alter the nearshore environments in which arctic anadromous fish spend part of their annual cycles.

By 1985, as outlined in the paper by Slaybaugh et al. introducing the Databank Project, investments by industry in analyzing the movements and other aspects of the biology of arctic anadromous fish had grown to unprecedented proportions for such a specialized subject. They are estimated to have reached $12 to $15 million by that year. Even this rate of investment promised to accelerate as a result of several further coastal developments then being planned. Also by 1985, contentions began to surface that further investigations were unnecessary because of the availability of existing data from completed surveys. Between 1970 and 1980, between two and 25 anadromous fish surveys had been conducted in the region each year (Fig. 1), many of which were funded by government agencies. At the beginning of the 1980s, the number of studies under way began to decline steadily, and those remaining were only the ones specifically required by regulatory agencies to be conducted by the petroleum industry. The scope of each of the dwindling number of monitoring studies grew to unprecedented proportions. More data were generated by a single study in 1985 than had been generated by some 50 studies in the decade 1970–1980 (Fig. 1).

An assessment of the situation by Standard Alaska Production Company (formerly Sohio Alaska Petroleum Company) led the company to allocate support for a review and "synthesis" project. Part of the synthesis was to be the formulation of a unified and distilled databank upon which contractors, regulatory agencies, and scientists could draw. This formal databank, after it was distilled from unpublished research reports and other forms of raw data, would be made accessible for pursuing further particular lines of investigation. Slaybaugh, Gallaway, and Baker's description of the databank is the first of nine papers in this volume, and it serves as a link between the two components of the Synthesis Project.

The other element of the Synthesis Project was to be the publication of a substantial body of analyses in refereed scientific literature. It was believed that debate about the major issues waged since the 1975 sealift-and-causeway episode had to be moved into the scientific arena, if the issues were ever to be resolved objectively. For the magnitude of the intended publication, a series that specialized in extended treatises was needed. Project leaders (including authors) approached *Biological Papers of the*

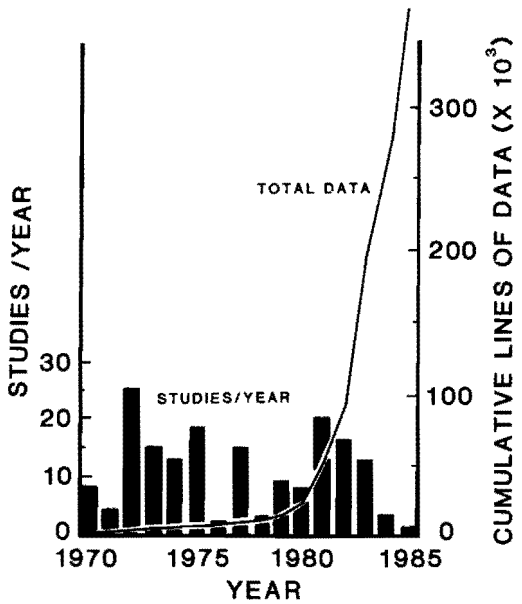

Figure 1. Historical trends in the conduct of anadromous fish studies in arctic Alaska and adjacent Canada, 1970–1985. The number of studies per year is the number of titles in the database. The number of lines of data, in thousands, is a cumulative total for data entered in the Databank for Arctic Anadromous Fish (DAAF-85). See Slaybaugh et al., this volume, for distinction between database and Databank.

University of Alaska in 1985–1986, and agreement was reached to collaborate in publishing contributions that passed the test of external peer review.

The eight papers that follow the one introducing the databank (Slaybaugh et al.) survived an external peer review process that ranged from straightforward critique by two disciplinary referees to complex multidisciplinary comments by as many as nine reviewers, some of whom actually represented teams of readers. Even before formal manuscripts were submitted, the authors of papers in this volume had presented their findings for critical exposures at a scientific meeting in Vancouver, British Columbia, in June 1986, and at a workshop in Anchorage in August of that year. These steps reflected the authors' and my own responses to the difficulties inherent in converting information that was predominantly in the form of file reports ("gray literature") into the form of traceable publications.

Organization of this series of contributions into a coherent sequence required more than casual effort. Readers of this volume, who must pick and choose which papers to read carefully, may find it useful to read the following paragraphs characterizing each of the papers and explaining their relations to the central issues.

First in this series of eight papers is Peter Craig's review of the strategy of anadromy, or amphidromy, in arctic fishes. It may be argued whether his contribution correctly interprets strategies; it cannot be argued that assessment of the effects of coastal intrusions on anadromous fishes is feasible in the absence of some interpretation of the adaptive value of these strategies.

In the following paper, Schmidt, Griffiths, and Martin present recent findings on the biological aspects of the impressive ability of arctic fishes to survive arctic winters. This paper pursues one of the important theses advanced in Craig's review, hence its placement here in the sequence. Our ignorance of how anadromous fishes use arctic winter habitats is nearly complete. This paper suggests some approaches to abating this ignorance.

The next paper returns to near the core of the issues that have defied resolution since 1975. Habitat utilization in the vicinity of artificial causeways has defined much of the debate underlying this volume. Robert Fechhelm and his coauthors make an in-depth analysis of data from the vicinity of the West Dock in Prudhoe Bay.

In 1983, a paper was published hypothesizing that all Arctic cisco populations in Alaska are migrants or strays from Canadian stocks that spawn only in the Mackenzie River drainage system (Gallaway et al. 1983, *Biol. Pap. Univ. Alaska* No. 21:4–23). So long as this hypothesis remains plausible, it affects the evaluation of the threats to Arctic cisco posed by causeways. As international resources dependent upon a single drainage system for their reproductive performance, the Arctic cisco populations in Alaska would be more affected by conditions along an obligatory migratory route to and from their habitats in arctic Alaska than if these populations originated from multiple stocks using widely dispersed drainages. Two papers in this sequence address the stock origin theory from different perspectives. Larry Moulton's paper examines the transport of young Arctic cisco along the coast and into the Colville River system in 1985. The paper by John Bickham and coauthors examines the stock origin theory for Arctic cisco from the genetic standpoint.

Advocacy for both sides of the issue (particularly that for prohibition of further causeway construction) has placed great emphasis on quantitatively defining summer habitats of anadromous fishes. This habitat evaluation has been carried out in terms of the dynamics of plumes and water mass characteristics, and responses of fish to these changes. Continued use or misuse of habitat evaluation procedures prompted Neill and Gallaway to write the next paper. More than one referee expressed delight that these authors dared to adopt such an unconventional approach in their numerical modeling exercise.

One of the justifications that could be made for the extraordinary levels of investment in studies of arctic anadromous fish is the importance of these fish stocks socially and culturally to native residents along the arctic coast. The next paper, by Peter Craig, is a review of what is known about subsistence use of anadromous fish stocks at coastal villages in arctic Alaska. This is an important interdisciplinary contribution, because the investigators who deal with subsistence harvest are traditionally quite separated from the biologists making environmental as-

sessments. The two groups have tended to use different methodology, their reports and documents have gravitated to distinct pools of gray literature, and Craig's paper attempts to bridge this gap.

The final paper in this volume is likely to be the one to draw the eventual critical judgment of scientists upon the whole collection. Gallaway, Gazey, and Moulton sum up their collective understanding about Arctic cisco in the form of a population model. The paper ventures long-range predictions about the populations of Arctic cisco as they will be sampled by the commercial fishery of the Colville River. The model presented in this paper is a synthesis of several of the current hypotheses. It stands as a testable statement on just how well the processes governing populations of arctic anadromous fishes are known. As this collection went to press, the fall 1988 fishery on the Colville River was yielding the low numbers of Arctic cisco predicted by the model (L. L. Moulton, J. W. Helmericks, pers. comm.).

Perhaps no challenging project is ever fated to turn out as originally conceived. This publication certainly did not. What began in the negative context of trying to rescue information from being lost nearly as fast as it was being gathered took on a more positive texture in two ways. First, the authors and I believe that there are some significant contributions to scientific understanding that have come to light in this collection. There are some globally intriguing aspects of the biology of arctic anadromous fishes. The very starkness of their existence is scientifically appealing. We would be gratified if this volume stimulates and sustains interest in these organisms among biologists distant from the Arctic. There are many other topics that could be developed and analyzed in addition to the small selection presented here. Second, we have been sustained by the belief in the "correctness" of making a start at publishing a portion of this information from a massive technical information base. We have considered ourselves pathfinders for others who may find themselves in parallel situations. We believe we have learned some things about how to distill something of lasting value from a large investment in technical studies, the results of which would languish otherwise in filing cabinets.

We cannot claim to have closed the information gap. During the 3 years it has taken to prepare the databank and the publication components of the original Synthesis Project, field investigations have continued on Alaska's North Slope. The number of data on arctic anadromous fishes collected annually has exceeded the total number collected in the entire previous decade. The fate of those expensive data is an unresolved question. Some would argue that it is time for the public sector or academia to step forth and assume responsibility for stewardship of this information.

It will be up to others to judge the merits of this collection and, in particular, to evaluate the wisdom of setting aside a portion of the cost of massive, continuing technical investigations for investment in synthesis and publication of results.

David W. Norton
October 1988

Biol. Pap. Univ. Alaska No. 24:4–26

The Databank for Arctic Anadromous Fish: Description and Overview

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Abstract. A search of documents reporting on arctic anadromous fish investigations conducted as early as 1771 and through the year 1985 yielded 280 references relevant to the ecology of arctic anadromous fish, mostly in the form of unpublished research reports and some supporting computer tapes of original data. These are referred to as the database. Of these, 96 individual studies were found to contain or be supported by sufficiently detailed research protocols that original data sets could be extracted and entered into a computerized Databank for Arctic Anadromous Fishes (DAAF-85). The content and organization of DAAF-85 are described in this paper, and the annotated list of references in the database is appended.

INTRODUCTION

There has been an explosion of information produced by investigations of arctic fishes since the early 1970s after oil was discovered on the Alaskan North Slope. Studies have expanded in size during this period such that the volume of information produced annually has increased at an accelerating rate. The greatest input of scientific information has occurred in conjunction with ongoing petroleum exploration and development operations. In compliance with the regulatory process, industry is required to conduct large-scale environmental surveys along the Beaufort Sea coast, particularly in the vicinity of Prudhoe Bay, Alaska.

The research effort to date has been substantial, and will likely continue to grow in the foreseeable future. Although specialists' understanding of arctic fishes has benefitted by this effort, it is becoming increasingly difficult to keep abreast of the accumulating information. Three factors contribute to this state of affairs:

1. "Gray literature"—With few exceptions, studies of arctic fishes have been reported only in government, industry, and consultant reports of limited distribution. As the years pass, it becomes more difficult to keep track of this diverse and obscure body of material.
2. Time constraints—Because of typically short contractual deadlines, fewer investigators have time to become familiar with all of the available information. As a consequence, it has become possible to draw contradictory conclusions about arctic fishes, depending upon which reports have been reviewed.
3. Personnel turnover—The problems posed by 1 and 2 above are compounded by short professional tenures of some scientists and agency personnel involved in arctic fish research and environmental impact analysis.

In summary, the rate at which information was lost or overlooked was approaching the rate at which it was acquired. These problems have contributed to a loss of efficiency for scientists, regulatory agencies, and the general decision-making system for arctic operations in which industry and government agencies participate.

In the context of these considerations, LGL Ecological Research Associates, Inc. (LGL), was contracted by Standard Alaska Production Company (SAPC) to compile arctic fish information through 1985 into a usable and accessible databank that was to focus on key species of anadromous fish, and to serve as a comprehensive source of primary data. The desired benefits of the databank were

1. Access—Resource management agencies require preparation and review of documents, such as scoping studies and oilspill response plans. Preparation and review of these documents put a premium on the ability of industry and agency scientists to retrieve all fish and fish-related environmental data available for a region or a site.
2. Increased efficiency—It was deemed desirable to reduce the time required to prepare background and comparative analysis sections for new projects.
3. Common database—By avoiding disparities in the availability of data to different investigators, it was hoped that a databank approach would reduce confusion arising from contradictory interpretations based on selections of noncorresponding data sets.

The Databank for Arctic Anadromous Fish (DAAF) was compiled over 2 years and was initially implemented on a microcomputer in the summer of 1986. Progress was reported at the June 1986 Arctic-Pacific Science Conference in Vancouver, British Columbia, organized by the American Association for the Advancement of Science. Following preliminary implementation of DAAF-85, a workshop was held in Anchorage, Alaska, to demonstrate

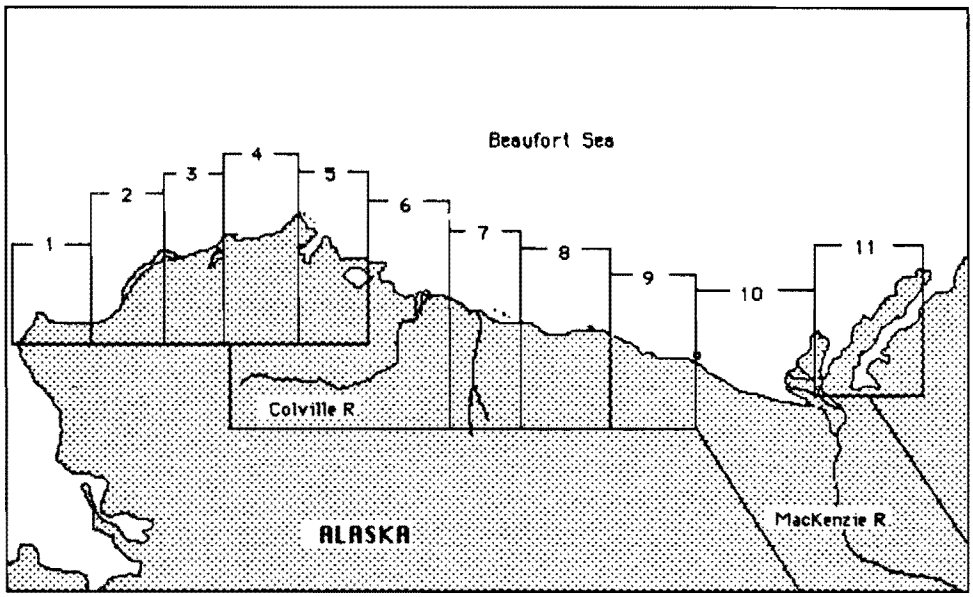


Figure 1. Study regions and their designation numbers, as used in the Databank for Arctic Anadromous Fish:

Region 1: Point Hope to Cape Beaufort;
Region 2: Cape Beaufort to Icy Cape;
Region 3: Icy Cape to Atanik;
Region 4: Atanik to Point Barrow;
Region 5: Point Barrow to Pitt Point;
Region 6: Pitt Point to Beechey Point;
Region 7: Beechey Point to Point Hopson;
Region 8: Point Hopson to Griffin Point;
Region 9: Griffin Point to Herschel Island;
Region 10: Herschel Island to Pullen Island;
Region 11: Pullen Island to Cape Dalhousie.

its utility and allow interactive use of the system by potential user groups. The workshop in August of 1986 was designed further to allow users to compare DAAF-85 outputs with the original source data contained in the paper copies of reports and publications, which were also available at the workshop. This workshop, hosted by the Arctic Institute of North America, was a component of the peer review process, to which SAPC wished the entire project to be subjected.

This paper describes the process of selecting, distilling, reconstructing, exercising quality control, and organizing the data that were taken from the database and entered into the Databank. For the benefit of readers who may not have access to the computerized Databank, an annotated list of the source materials in the database is appended.

METHODS

Scope of the Database

At the outset of sifting through the entire body of information relating to arctic anadromous fishes, geographic and taxonomic filters or limits were erected. Geographically, data were included from studies that took place wholly or in part between Point Hope, Alaska, in the northeastern Chukchi Sea, and Cape Dalhousie on the Tuktoyaktuk Peninsula in the Canadian portion of the Beaufort Sea (Fig. 1). Taxonomically, selection of data for review and possible inclusion emphasized five species of anadromous fish. These species were emphasized because of their importance in subsistence or commercial fisheries in the study area, and because resource management agencies had identified them as potentially affected by petroleum development operations:

Arctic char (*Salvelinus alpinus*)—This is the western arctic form of the Arctic char, *S. alpinus*, considered synonymous with the northern form of the Dolly Varden, *S. malma*;
Arctic cisco (*Coregonus autumnalis*);
Least cisco (*C. sardinella*);
Broad whitefish (*C. nasus*);
Humpback whitefish (*C. pidschian*).

Data Review and Selection

The first step in constructing the Databank for Arctic Anadromous Fish (DAAF-85) was to search the available literature for information. Just over 1,200 reports, publications, and documents were reviewed at various levels of detail. These bore dates from 1771 to the end of 1985. Of these, 280 were found to contain geographically and taxonomically relevant material worthy of a careful second screening of the full text and documentation of original data. Many of the more than 900 reports were rejected in the initial screening on the basis of information in abstracts or summaries. Reasons for disqualifying ma-

terial that had met the geographic and taxonomic screening criteria included

1. Works were review papers not containing original data;
2. Studies dealt with nonecological subjects, such as taxonomy;
3. Works were considered to be of low or unverifiable quality;
4. Studies were based on closed freshwater lake systems, hence dealt with populations of landlocked, or nonanadromous fish.

The 280 citations that survived this screening constitute what we refer to as the database.

The database was further screened to select the most important and informative reports on scientific work conducted in arctic Alaska and Canada. Within the constraints of time and available funding, we sought a balance between efficiency and inclusiveness in the transfer of data from the database to the Databank itself. The resulting balance produced 96 primary references or data sources from the 280 listed in the database. The reasons for finally excluding each of 184 (66%) of the entries in the database from transfer to the Databank are documented in the annotated database (Appendix A). There were six types of reasons for exclusion (numbers of entries excluded):

A. Reference may contribute information, but judged to be of lower priority than other sources for such reasons as low volume of data, lack of methodological documentation, years elapsed since study conducted, etc. (39);
B. Useful reference, but based on nonprimary data (e.g., mainly a review paper), original data not recoverable, or data not convertible to ecological context (53);
C. Reference proved to be redundant with, or superseded by, another reference (17);
D. Data proved to be from outside the geographic region prescribed (11);
E. Source document proved to be inappropriate source of data for arctic anadromous fish (40);
F. Document or its supporting original data proved unobtainable with reasonable time or effort (24).

Data Formatting and Quality Control

Upon selection of source material for the Databank (DAAF-85), the data had to be integrated into a common format for access. As a consequence of the high rate of production of data in the vicinity of Prudhoe Bay by relatively few studies between 1981 and 1985, almost 90 percent of the volume of data to be entered into the Databank was available in one or another computerized format (digital tapes, disks, etc.). Computer transformation and translation programming took care of large blocks of these transfers to the Databank. The remaining 10 percent required physical transcription to the Databank format from paper copies of original reports and supporting documentation.

While preparing the DAAF-85 formats and initially entering data from the various sources, we discovered great variation in conformance to conventional scientific organization and documentation. Studies, and the data available from them, ranged from high-quality investigations to poorly documented sampling efforts. Poor documentation commonly involved inattention to quality control that produced coding errors in archived records and tapes of sampling data. It was not our intention to perpetuate mathematical errors or other questionable information in DAAF-85. Recognizing that the credibility and utility of the Databank depended on the accuracy of the data entered, we found it necessary to expend considerable effort both in verifying or correcting original source data (whenever original investigators could be reached), and in exercising in our own quality control. First, we found that the task of encoding and transforming data could not be accomplished satisfactorily by technicians. Rather, it required an understanding of experimental designs and methodologies of original studies, combined with an understanding of the ecology of arctic fishes, to detect and sort out inconsistencies or technical questions with each data source. Consequently, this phase of the project was conducted by biologists directly familiar with arctic fish research through their own conduct of many studies in the Arctic. After the data were encoded, all data records were subjected to two verification procedures. Computer printouts were compared line-by-line to the data presented in the original reports and then were processed with programs designed to detect errors.

Throughout the encoding and verification steps, we were careful never to assign a level of detail to a data set any finer than that provided by the original author. If the author merely reported the total number of fish taken during a particular survey, only that total number is available from the Databank. The trend over the years has been for observers to record, archive, and report sampling data in increasing detail, and the Databank reflects this historical trend.

File Types for Data

Data were divided into nine major categories (file types):

species composition;
length frequency;
age frequency;
sexual maturity;
reproduction (fecundity, egg size, gonad weight, etc.);
length–weight relationships;
mark–recapture data;
diet;
physical data.

Physical data include only information collected in direct conjunction with biological surveys. With the excep-

tion of the species composition files, the remaining biological data file types provide data on only five targeted anadromous fish species.

The species composition files provide numerical abundance data for all species of fish, whether they are of marine, anadromous, or freshwater origin. Inclusion in the Databank of species composition data was not decided on the sole criterion of presence of one of the five targeted species, because if a survey location was judged to be accessible to anadromous fish, their absence is just as informative as their presence.

Access to Files

Anticipating the various motivations of users, we designed the Databank to yield information in response to several types of inquiries.

Source of data. Each research report or study in the database was assigned a number (see Appendix A). A user can retrieve all information derived from a particular research report, thereby facilitating verification of the accuracy and completeness of our data entry.

Sampling sites. Within each study the data are further organized by specific sampling station number. DAAF-85 provides a digitized map of the area surveyed by a particular study, including sampling station locations. Sampling site designations are cross-referenced to match the Databank station designations with those presented in the original report. Each map provides the literature citation, the nature of the source—whether a report or a computer tape—and lists the number of data lines for each file type for each of the five species targeted for emphasis.

Region. Data for each study are also assigned a region number from 1 (Point Hope) to 11 (Cape Dalhousie). A user interested only in the data available associated with the Mackenzie River, for example, can call up all data for that region by using the Region 10 access code (Fig. 1).

Species. Except for the species composition and physical data files, as described above, data can be accessed for any one of the five targeted species only, by specifying the species of interest.

Date. A user interested in data collected at a particular time or time interval, for some reason, can query the Databank by specific dates or time intervals. The data conform to the level of detail provided by the original author, as stated above.

Gear type. A description of the sampling gear used to collect field data is also provided. Within the Databank, gear type is designated by a numeric code. This code listing can be looked up at any time.

File-specific coding. It was further necessary to provide record-specific variables for the biological data file types. For example, each data line in the length frequency file has entries specifying the type of length measurement reported. The comparability of separate data sets is affected by whether fork length, standard length, or total length is reported. Within each type of length measurement, intervals are specified, and numbers of fish per interval, percent frequency of fish per interval, mean lengths, and standard deviations are all displayed. A detailed description of data contained within each file type can be found in a User's Guide to the Databank. That Guide is maintained on-site with DAAF-85 (and later versions) and can be requested from the senior author.

RESULTS

Synopsis of Completeness of Data by Region and File Type

For each of the seven major biological categories or file types, it is instructive to query the Databank on the distribution of data availability, sorted by region and by species. Results of this output from the Databank are given in Figures 2 through 8. In these figures, the numbers in each cell of the matrix are the assigned study numbers corresponding to the numbers in Appendix A.

For each biological file type, the largest concentration of studies has been conducted in Regions 6 and 7 (Harrison Bay and Prudhoe Bay, Alaska). This concentration of data results from continuous surveys of Alaskan waters conducted by the Alaska Department of Fish and Game, and subsequently the numerous environmental studies conducted in the Prudhoe Bay region in response to petroleum development.

The second largest regional concentration of data available in the Databank is that of the Mackenzie River drainage, Regions 10 and 11. This concentration reflects the Mackenzie River's status as the largest freshwater drainage in the North American Arctic, and as a key system for both anadromous and freshwater fishes. Examination of the titles and of studies listed in Appendix A reveals an interesting historical trend. Many of the early data are associated with surveys conducted in various tributaries of the Mackenzie River, but in recent years the focus has shifted to coastal waters both east and west of the mouths of the Mackenzie River.

Far fewer data of all types are available for the Chukchi Sea coast west of Point Barrow (Regions 1–4; Fig. 1). This geographic area has not yet proven to be an important source of petroleum reserves and thus has generated less environmental interest than the central Beaufort Sea and the Mackenzie River.

The most comprehensive biological data fall under the category of species composition (Fig. 2) because most surveys at least report total numbers of specimens caught. The second most abundant data represented in the Databank are from reported length frequency relationships (Fig. 3). Comparison of Figures 2 and 3 shows that substantially fewer studies reported length frequency data

REG	ARCTIC CISCO	LEAST CISCO	CHAR	BROAD WHITEFISH	HUMPBACK WHITEFISH
1					
2	.11,39,40,67	.11,39,67,103	.11,39,40,67	.11,39,67,103	.11,39,67,103
3	.39,67	.39,67,103	.39,67	.39,67,103	.39,67,103
4	.67	.67,103	.67	.67,103	.67,103
5	.39,67,136,163	.14,39,67,103,130, .136,145,163	.14,39,67,163	.14,39,67,103, .145,163	.39,67,103,136, .145,163
6	.10,11,32,34,39, .67,78,79,95,136 .152,163	.10,11,14,32,34, .39,67,78,79,95, .103,136,163,164	.10,11,13,14,32, .34,39,67,78,79, .95,152,163,154	.10,11,13,14,32, .34,39,67,78,79, .95,103,136,152, .163	.10,11,32,34,39 .67,78,79,95,103, .136,152,163
7	.10,28,32,34,35, .55,63,78,136,298	.10,14,28,32,34, .35,55,63,78,136, .164,298	.6,10,14,15,28 .30,32,34,35,36, .55,63,78,92,134, .135,141,164,298	.10,14,28,32,34, .35,55,63,78,136, .298	.10,32,34,35,55, .78,136,298
8	.10,28,32,35,39, .63,111,147,151	.10,28,32,35,39, .63,147,164	.10,28,32,35,36, .39,63,111,122, .140,147,151,164	.10,28,32,35,39, .63	.10,32,35,39
9	.35,61,62,63,111, .147	.35,61,62,63,85, .147	.35,60,61,62,63, .111,122,140,143	.35,63	.35
10	.35,44,46,72,74, .76,80,105,125, .142,146,165	.8,35,36,44,46, .72,74,76,125, .142,165	.35,44,46,72,74 .76,80,86,105,125, .142,146,165	.35,44,46,72,74, .76,105,125,142, .165	.35,44,46,72,74, .76,105,125,142, .165
11	.18,24,57,69,75, .80,105,114	.18,24,57,69,75, .80,105,114,138	.8	.18,24,57,69,75, .80,105,114,138	.24,75,105,114

Figure 2. Sample printout of record types in the Databank (DAAF-85): studies that reported species composition by region and by species. Numbers in each cell refer to study numbers listed in Appendix A for each reference used in the Databank.

REG	ARCTIC CISCO	LEAST CISCO	CHAR	BROAD WHITEFISH	HUMPBACK WHITEFISH
1					
2		.103		.103	.103
3		.103		.103	.103
4		.103		.103	.103
5	.163	.14,103,130,136, .145,163	.14,163	.14,103,136,163	.103,136,145,163
6	.10,34,79,95,152, .163	.10,14,34,79,95, .103,135,152,163, .164	.10,13,14,32,34, .79,95,103,163	.10,14,32,34,79, .95,103,136,163	.10,32,34,79,95, .103,136,163
7	.10,35,63,111, .147,151	.10,63,164	.10,28,32,63,111, .122,140,147,151, .164	.10,32,63	.10,32
8	.10,35,63,111, .147,151	.10,63,164	.10,28,32,63,111, .122,140,147,151, .164	.10,32,63	.10,32
9	.35,61,62,63,111, .147	.62,63	.60,61,62,63,111, .122,140,147	.10,32,63	.10,32
10	.35,44,72,76,80, .105,142,146	.44,76,80,105, .142,146	.72,76	.44,72,80,105, .142,146	.44,72,105,142
11	.18,24,57,69,75, .80,105	.18,24,57,69,75, .80,105,138		.18,24,69,75,80, .105,138	.24,75,105

Figure 3. Sample printout of record types in the Databank (DAAF-85): studies that reported data on length frequency by region and by species. Numbers in each cell refer to study numbers listed in Appendix A for each reference used in the Databank.

REG	ARCTIC CISCO	LEAST CISCO	CHAR	BROAD WHITEFISH	HUMPBACK WHITEFISH
1					
2					
3					
4					
5		.145			
6	.10,34,78	.10,34,78,164	.10,34,78,164	.34,78	.78,79
7	.10,34,35,55,63, .78	.10,34,55,63,78, .164	.6,28,30,34,55, .63,78,92,134, .135,164	.34,78	.78
8	.10,35,63,111,147	.10,63,164	.28,63,111,122, .147,164		
9	.35,62,63,111,147	.62,63,85	.60,62,63,111, .122,147		
10	.35,44,76,80,105 .142,146,165	.44,76,80,85,105, .142,146,165	.8,44,72,76	.80,105,142,146 .165	.44,72,76,105, .142,165
11	.18,57,69,75,80 .105	.18,57,69,75,80 .105,138	.8	.18,69,75,80,105, .138	.75,105

Figure 4. Sample printout of record types in the Databank (DAAF-85): studies that reported data on age frequency by region and by species. Numbers in each cell are study numbers (see Appendix A).

than reported species composition. This trend of decreasing data availability continues through the series of biological file types: age frequency (Fig. 4), diet (Fig. 5), sexual maturity (Fig. 6), reproduction (Fig. 7), and length–weight relationships (Fig. 8).

These summaries of the contents of the Databank illustrate where scientific efforts have focused regionally, and illustrate some of the biological relationships of arctic anadromous fishes that have received the least attention.

Examples of Use of the Databank

To illustrate the range of graphic outputs of which DAAF-85 is capable, we reproduce a selection of examples that informed users might wish to see. We envision users progressing from general toward more specific sorts of data selection. Later, with increasing facility at negotiating through the Databank procedures, users can begin to compare specific biological parameters among years, dates, regions, or sites.

In brief, a DAAF-85 user progresses through a set of four menus to gain access to the information available from the integrated data. First is a "procedure" menu, from which the first option is "display records." Next, the user is asked to specify record type from a menu of that title, within which the nine file types are the options. The third menu level specifies acccess type, from which the options include everything from viewing a specific record to scrolling sequentially through all records specified at the previous level. Finally, the user can choose options from the key specification menu that specify the level of detail desired in the information to be retrieved.

REG	ARCTIC CISCO	LEAST CISCO	CHAR	BROAD WHITEFISH	HUMPBACK WHITEFISH
1					
2					
3					
4					
5		.145			.145
6	.10,34,78	.10,34,78	.10,34,78	.78	.78
7	.10,34,35,55,63, .78	.10,34,55,63,78,	.10,28,30,34,55, .63,92,135,164	.55,78	.78
8	.10,35,63,147	.10,63	.10,28,63,147,164		
9	.35,61,62,63,147	.63,85	.60,61,62,63,147		
10	.35,44,72,76,80, .105,142	.44,72,76,80,85, .105,142,165	.8,72,76	.44,73,105,142, .165	.44,72,76,105, .142,165
11	.18,75,80,105	.18,75,80,105,138	.8	.18,105,138	.105

Figure 5. Sample printout of record types in the Databank (DAAF-85): studies that reported data on diet, by region and by species. Numbers in each cell are study numbers (see Appendix A).

REG	ARCTIC CISCO	LEAST CISCO	CHAR	BROAD WHITEFISH	HUMPBACK WHITEFISH
1					
2					
3					
4					
5		.145	.14		.145
6	.34,79,95	.34,78,95,164	.14,34,78,95,164	.34,78,95	.78,79,105
7	.34,35,55,63	.34,55,63,78,164	.14,28,30,34,55, .63,78,135,164	.34,78	.78
8	.35,63,111	.63,104	.28,63,111,164		
9	.25,62,63,111	.62,63,85	.60,62,63,111		
10	.35,44,46,76,105, .146,165	.44,46,76,85,86, .105,146,165	.8,44,46,76	.46,86,105,146, .165	.44,46,76,86,105, .165
11	.18,75,105	.18,75,105	.8	.18,75,105	.75,105

Figure 6. Sample printout of record types in the Databank (DAAF-85): studies that reported data on sexual maturity, by region and by species. Numbers in each cell are study numbers (see Appendix A).

For example, a user could begin by obtaining an overview of the relative density of information available from studies yielding species composition data conducted in the vicinity of Prudhoe Bay. The result of such a general "display records" inquiry is shown graphically in Figure 9A. A total of 26 different studies specific to that region is contained in DAAF-85. Should the user want an indication of how these 26 studies were distributed over the years, this information can be displayed by combining display-records procedure, species composition record type, and an access type specification for date of studies, as in Figure 9B. This combination of options shows the user that the original source documents date from 1972, and that new data have been added each year for this region through 1985. The identities of original sources of data on species composition from studies conducted around Prudhoe Bay can be listed, as they were above in Figure 2.

By backtracking and substituting other options at the level of the menu for record type, the user interested in Prudhoe Bay information can convince himself that of the studies reporting species composition, fewer reported length frequency relationships (Fig. 10A), and fewer still reported age frequency relationships (Fig. 10B). This is an alternative way of displaying information similar to that shown above in Figures 2, 3, and 4.

Another line of more detailed inquiry might be that of a user interested in a particular location within the Prudhoe Bay region. To get an idea of how sampling sites were arrayed with respect to a location, the user might specify a combination of two gear types (e.g., net and fyke trap) and might further specify only the inclusion of four sampling seasons, 1981 through 1984. The results of such multiple specifications are shown in Figure 11. The ultimate level of detailed data retrieval from DAAF-85 is illustrated by Figure 12. Here, a user has had his interest drawn to a single sampling site, a single date in 1981, one record type, a specific gear type, and to Arctic cod as the species of choice. Having filtered out all less focused information, the user might ponder the significance of this difference in catch between the western and eastern sides of the sampling gear on 22–23 August 1981.

REG	ARCTIC CISCO	LEAST CISCO	CHAR	BROAD WHITEFISH	HUMPBACK WHITEFISH
1					
2					
3					
4					.145
5		.145			
6	.34	.34			
7	.34,35	.34	.28,30,55,92,135		
8	.35		.28		
9	.35,62		.60,62		
10	.35	.44,105	.8	.44	.44
11		.138	.8	.138	.165

Figure 7. Sample printout of record types in the Databank (DAAF-85): studies that reported data on reproduction, by region and by species. Numbers in each cell are study numbers (see Appendix A).

REG	ARCTIC CISCO	LEAST CISCO	CHAR	BROAD WHITEFISH	HUMPBACK WHITEFISH
1					
2					
3					
4					.145
5		.130,145	.14		
6	.152	.152	.13,14,152		
7	.35		.14,28,30		
8	.35		.28,140		
9	.35,62	.62,85	.60,62		
10	.35,44,72,142,146	.44,85,142,146,165	.8,72	.44,72,142,146,165	.44,72,142,165
11	.69	.69,138	.8	.138	.165

Figure 8. Sample printout of record types in the Databank (DAAF-85): studies that reported data on length–weight relationships by region and by species. Numbers in each cell are study numbers (see Appendix A).

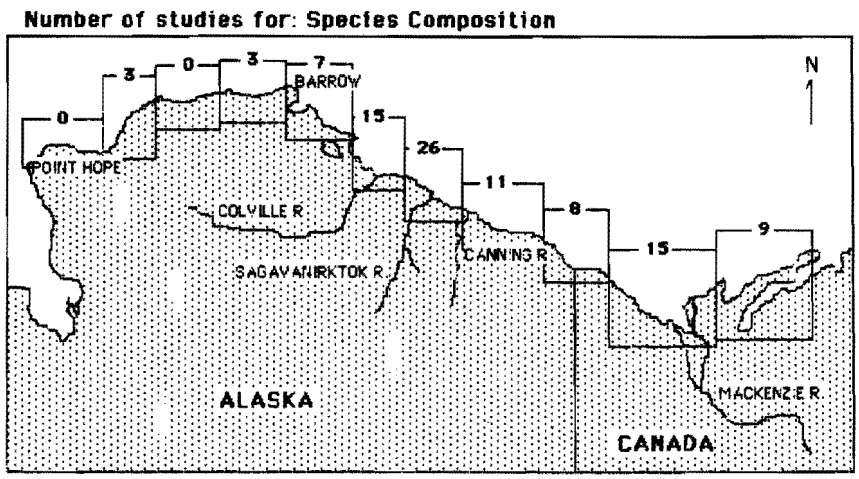
By contrast with such specificity, another user might elect to scan the age structure of all Arctic cisco caught in the three Canadian Beaufort Sea regions covered by DAAF-85, to see how age frequency relations there compared with those from western regions. The results of this composite graphic display are shown in Figure 13.

The versatility of the Databank, as shown in these examples (Figs. 9–13) is admittedly limited to those regions, record types, and sampling strategies that have attained a critical threshold of research attention. As DAAF-85 is succeeded by later versions, this limitation presumably will be relaxed.

DISCUSSION

Compilation and use of the Databank for Arctic Anadromous Fish (DAAF-85) has been an informative exercise. We believe that DAAF-85 is a useful compilation, because it can be approached by users with a wide variety of motivations and interests. It can serve a user interested in specific catch data at a given location within a given field season and a user interested in a coastwide synopsis of available information over a span of many years. Specificity of data in DAAF-85 is limited only by the detail provided by original investigators. The data in DAAF-

A



B

	1954	1972	1973	1974	1975	1976	1977	1979	1980	1981	1982	1983	1984	1985
Region: 1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Region: 2	-	-	-	-	-	-	-	-	-	-	1	-	1	1
Region: 3	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Region: 4	-	-	-	-	-	-	1	1	-	-	1	-	-	-
Region: 5	1	-	-	-	-	-	1	1	-	-	2	-	1	1
Region: 6	-	1	-	2	-	-	-	3	-	4	2	1	2	-
Region: 7	-	3	1	3	1	1	2	2	1	3	2	3	3	1
Region: 8	-	1	-	2	-	-	2	1	-	1	2	-	2	-
Region: 9	-	1	-	3	1	-	1	-	-	-	-	1	1	-
Region: 10	-	1	3	4	4	1	1	-	-	-	1	-	-	-
Region: 11	-	-	1	-	-	-	1	1	1	-	1	2	1	1

Figure 9. Samples of output by the Databank (DAAF-85): number of studies in each of 11 regions reporting species composition data. **A.** Numbers of original source reports by region. **B.** Numbers of original source reports by date and by region.

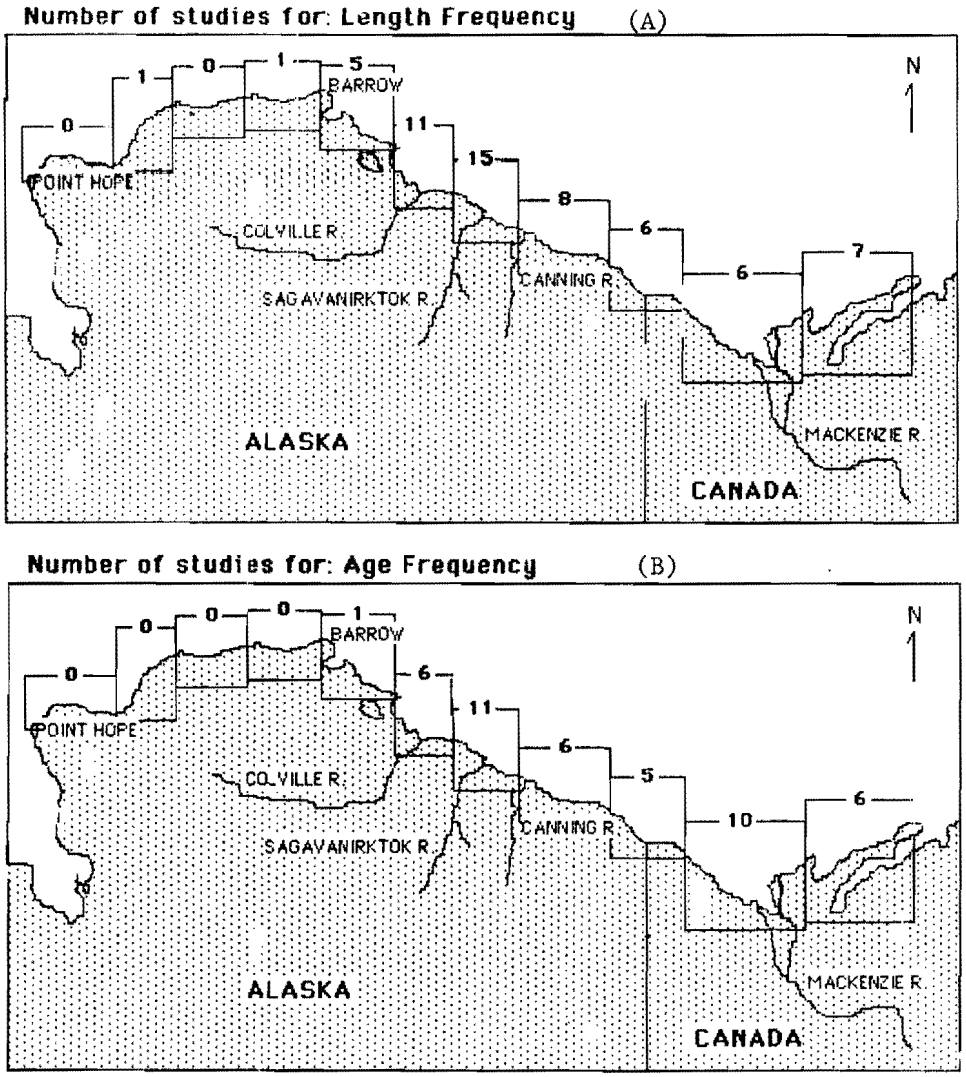


Figure 10. Samples of output by the Databank (DAAF-85): number of studies in each of 11 regions reporting specified file types. **A.** Total original source reports furnishing data on length frequency by region. **B.** Total original source reports furnishing data on age frequency by region.

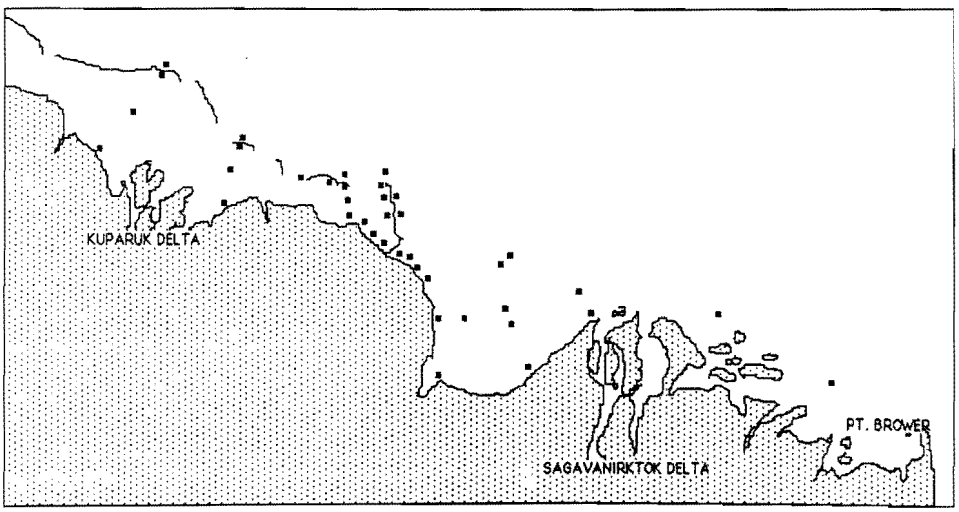


Figure 11. Graphic output by the Databank (DAAF-85), showing all net and fyke trap sampling sites used by various studies from 1981 through 1984 in the vicinity of Prudhoe Bay.

LENGTH FREQUENCY

Study : 64 Region : 7 Station : PRUD13 Direction : E Gear : F02

Start Date : AUG 22 1981 Total Catch : 28 Habitat : C
End date : AUG 23 1981 Total effort (days) : 1 Species : ARCD

Length measurement type : F

Length	Freq.
160 - 169	1
180 - 189	2
120 - 129	3
110 - 119	2
210 - 219	1
140 - 149	1
130 - 139	6
150 - 159	5
170 - 179	1
80 - 89	2
220 - 229	2
90 - 99	1
70 - 79	1
-	
-	
-	
-	

LENGTH FREQUENCY

Study : 64 Region : 7 Station : PRUD13 Direction : W Gear : F02

Start Date : AUG 22 1981 Total Catch : 19 Habitat : C
End date : AUG 23 1981 Total effort (days) : 1 Species : ARCD

Length measurement type : F

Length	Freq.
120 - 129	2
140 - 149	3
190 - 199	1
170 - 179	2
80 - 89	3
90 - 99	1
200 - 209	1
110 - 119	2
130 - 139	2
150 - 159	1
100 - 109	1
-	
-	
-	
-	
-	
-	

Figure 12. Sample of highly detailed DAAF-85 output: length frequency data file type, for one species (Arctic cod), at one sample station for one day's effort, for one gear type.

85 are organized into an integrated structure resulting from the conversion of all data into standard formats. This conversion process involved standardization of several types of information: codes (species, gear types, etc.), calculations (catch-per-unit-effort, length increments), and summary variables (dates, net directions). Specific data are retrievable using any of these variables as a central focus.

Compilation and quality control applied to DAAF-85 have revealed some noteworthy historical trends in applied studies of arctic anadromous fishes. The very contrast between the two types of original sources of data, for example, reflects the changing nature of environmental studies in the North American Arctic. In numbers of original studies, the majority that contributed to DAAF-85 were available only in printed document form. By contrast, the greatest number of data lines in DAAF-85 (about 90%) came from the fewer, more recent studies for which original data were available in computer tape formats. Increasing power to generate increasingly de-

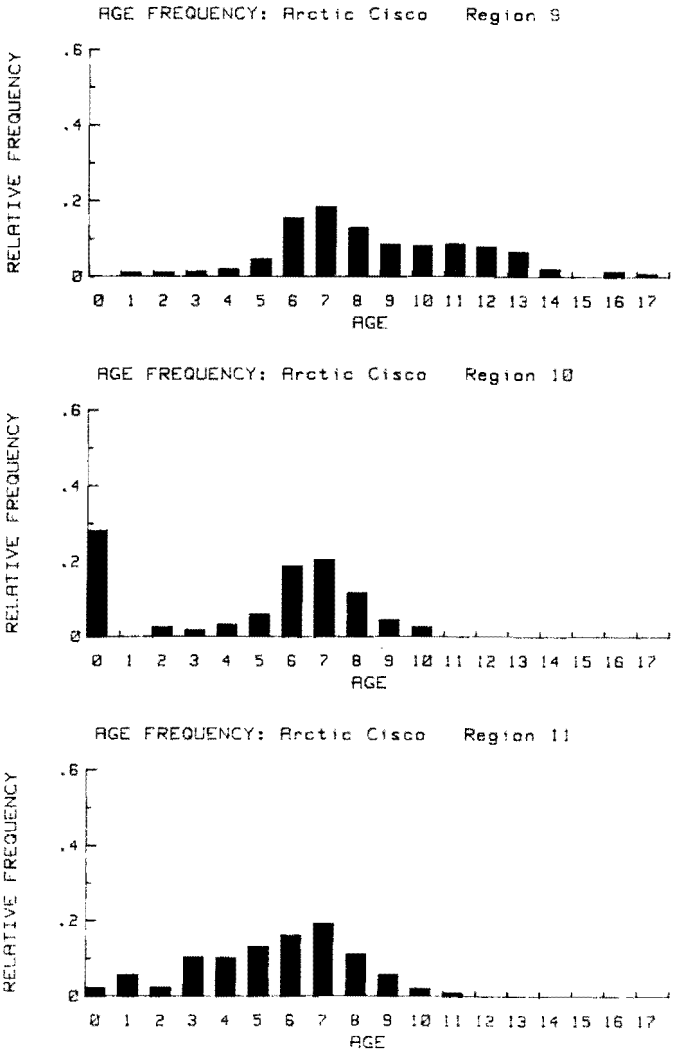


Figure 13. Composite of histograms for three eastern regions covered by DAAF-85, comparing age frequency relationships of all Arctic cisco sampled and reported on between 1972 and 1985.

tailed information is concentrated in the hands of a smaller number of investigators as time passes. Our translation of original data tapes into the format for DAAF-85 showed that these tapes are not error-free. In fact, they are subject to some new types of errors that arise at the encoding and digitization stages, when investigators' field notes are converted to tape formats. These trends and developments tend to put a premium on vigilance and quality control by teams of investigators and their contract supervisors.

As the authors were completing this discussion (summer, 1988) the results of just four studies conducted after 1985 have doubled the numbers of lines of data eligible to be included in updated versions of DAAF-85. Through funding by Standard Alaska Production Company, these data are being incorporated into the original version of DAAF-85 (which will be designated with updated version numbers as subsequent years of data are incorporated, e.g., DAAF-86 when all data sets through the 1986 field season are entered).

With the accelerating growth of the volume of data to be included in DAAF, this Databank has outgrown the capacity of microcomputers to house the information, so it is now installed on the Standard Alaska Production Company's mainframe computer in Anchorage, Alaska. It is managed by computer-specific software for that system. Because of the continuing evolution and updating of the system and the contents of DAAF, persons interested in access to the data are advised to contact the senior author for timely advice on access and availability.

As outlined at the beginning of this overview, the problem of information loss was a serious concern and motivation for this work. We believe that the experiences to date with the database and conversion to DAAF-85 demonstrate the feasibility of treating the problem as outlined. This database–DAAF-85 approach has resulted in a body of regional information that is in our experience considerably more tractable than databases compiled on a national scale. We suggest that this regional approach may be a successful model for others to emulate, particularly in arctic North America.

In this instance, a single petroleum company has taken the initiative to arrest the loss of information that was acquired at great cost to several government agencies and several private corporations. The intended contribution by this entire project is to take the first steps to ensure the continued availability of this information to the scientific community. Although we have shown the technical feasibility of information salvage from such a body of fast-paced environmental studies, this salvage nevertheless requires a significant dedication of personnel and resources over a period of time.

The ultimate responsibility for archival and retrieval of data of public interest, such as those contained in DAAF-85 and later versions, is an interesting contemplation. Traditionally, such responsibility for nonproprietary information has rested with either the public (as opposed to private) sector, or is borne by the academic community. It may be unwise for the academic community to count on the continued public-spirited contribution by a single petroleum company to the stewardship of this information. Alternatives should at least be discussed.

Finally, we note that the existence of information in an integrated Databank such as DAAF-85, however useful and used, cannot be a complete substitute for the original study reports or publications. Responsible use of DAAF-85 still requires an understanding of details, such as techniques and interpretations, contained in original sources. It is not up to a Databank, but to people, to conduct analyses and draw conclusions. The Databank, however, can provide the impetus for hypotheses, expand the breadth and depth of knowledge, and provide a background for planning future studies.

APPENDIX A. ANNOTATED MASTER LIST OF SOURCES OF INFORMATION IN THE DATABASE

This alphabetic–chronological master list includes the reference study numbers of all studies reviewed through July 1986. (A master list of sources sorted by study reference number is maintained with DAAF-85, or may be obtained by writing the second author of this overview paper.) Reasons that studies were reviewed but not entered into the Databank for Arctic Anadromous Fish (DAAF-85) are indicated by a letter code following their reference study number. Codes:

A. May contribute information, but of lower priority than other sources;
B. May be a useful reference, but lacks original data (e.g., a review paper) or is a taxonomic or other nonecological study;
C. Redundant with, or superseded by, another reference, which is indicated by study number, in parentheses;
D. Outside the study boundaries;
E. Inappropriate data source for arctic anadromous fishes;
F. Could not be obtained in time for review.

	Reference Number and Code
Able, K., and D. McAllister. 1980. Revision of the snailfish genus *Liparis* from arctic Canada. Can. Bull. Fish. and Aquat. Sci. 108 pp.	1[B]
Abrahamson, G. 1963. Tuktoyaktuk–Cape Parry area economic survey. Rep. by Indust. Div., Can. Dep. North. Affairs Natl. Resour., Ottawa. 89 pp.	166[E]
Alt, K. T. 1972. A life history study of sheefish and whitefish in Alaska. Alaska Dep. Fish and Game, Annu. Rep. 12:1–31.	3[D]
Alt, K. T. 1973. Contributions to the biology of the Bering cisco (*Coregonus laurettae*) in Alaska. J. Fish. Res. Board Can. 30:1885–1888.	167[A]
Alt, K. T. 1976. Age and growth of Alaskan broad whitefish, *Coregonus nasus*. Trans. Am. Fish. Soc. 105:526–528.	4[A]
Alt, K. T. 1979. Contributions to the life history of the humpback whitefish in Alaska. Trans. Am. Fish. Soc. 108:156–160.	5[A]
Alt, K. T., and R. Furniss. 1976. Inventory and cataloging of North Slope waters. Alaska Dep. Fish and Game. Federal Aid in Fish Restoration, Annu. Rep. of Prog. 17:129–150.	6
Alt, K. T., and D. R. Kogl. 1973. Notes on the whitefish of the Colville River, Alaska. J. Fish. Res. Board Can. 30:554–556.	2[C] (78)
Andriyashev, A. P. 1954. Fishes of the northern seas of the U.S.S.R Isvestiya Akademii Nauk SSSR. Translation from Russian: Israel Program for Scientific Translations, 1964, Jerusalem, Israel.	168[D]
Armstrong, R., and J. Morrow. 1980. The Dolly Varden charr. Pages 99–140 *in* E. Balon, ed. Charrs: Salmonid fishes of the genus *Salvelinus*. Dr. W. Junk bv. Publishers, Hague, Netherlands.	7[B]
Atkinson, C. 1976. Development and potential yield of arctic fisheries. Chapter 24 *in* D. W. Hood and D. C. Burrell, eds. Assessment of the arctic marine environment, selected topics. Inst. Mar. Sci., Univ. Alaska, Fairbanks, Occas. Publ. No. 4. 468 pp.	87[E]
Bain, L. H. 1974. Life histories and systematics of arctic char (*Salvelinus alpinus* L.) in the Babbage River system, Yukon Territory. M.Sc. Thesis, University of Calgary, Calgary, Alberta. 156 pp. [Also: Arctic Gas Biol. Rep. Ser. 18(1). 156 pp.]	8
Bain, L. H., and A. D. Sekerak. 1978. Aspects of the biology of Arctic cod, *Boreogadus saida*, in the central Canadian Arctic. Rep. for Polar Gas Project, by LGL Environ. Res., Toronto, Canada. 104 pp.	26[E]
Barlishen, W. J., and N. T. Webber. 1973. A history of attempts to commercially fish the Mackenzie River Delta, N.W.T. A submission prepared for section three of the Federal–Territorial Task Force Report on Fisheries Development in the Northwest Territories. MS. Rep. 22 pp.	172[E]
Bean, T. 1887. The fishery resources and fishing grounds of Alaska. Pages 81–115 *in* The fisheries and fishing industries of the United States. Section III. Government Printing Office, Washington, D.C.	149[A]
Bendock, T. 1976. De-watering effects of industrial development on arctic fish stocks. Rep. to Alaska Board of Fish. by Alaska Dep. Fish and Game, Fairbanks, Alaska. 13 pp.	9[A]
Bendock, T. 1977. Beaufort Sea estuarine fishery study. *In* Environ. Assess. Alaskan Cont. Shelf. BLM/NOAA, OCSEAP, Boulder, Colorado, Annu. Rep. Prin. Invest. 45 pp.	175[C] (10)
Bendock, T. 1979a. Beaufort Sea estuarine fishery study. *In* Environ. Assess. Alaskan Cont. Shelf. BLM/NOAA, OCSEAP, Boulder, Colorado, Final Rep. Prin. Invest. 4:670–729.	10
Bendock, T. 1979b. Inventory and cataloging of arctic area waters. Alaska Dep. Fish and Game, Annu. Perform. Rep. 20:1–64.	11
Bendock, T. 1980. Inventory and cataloging of arctic area waters. Alaska Dep. Fish and Game, Annu. Prog. Rep. 21:1–31.	12[F]
Bendock, T. 1981. Inventory and cataloging of arctic area waters. Alaska Dep. Fish and Game, Annu. Perform. Rep. 22:1–33.	13

Bendock, T. 1982. Inventory and cataloging of arctic area waters. Alaska Dep. Fish and Game, Annu. Prog. Rep. 23:1–43. 14

Bendock, T. 1983. Inventory and cataloging of arctic area waters. Alaska Dep. Fish and Game, Annu. Rep. 24:1–28. 15

Bendock, T., and J. Burr. 1980. Index to North Slope stream and lake surveys. Alaska Dep. Fish and Game, Fairbanks, Alaska. 176[C] (137)

Bendock, T., and J. Burr. 1984a. Inventory and cataloging of arctic area waters. Alaska Dep. Fish and Game, Annu. Rep. 25:1–46. 136

Bendock, T., and J. Burr. 1984b. Freshwater fish distributions in the central arctic coastal plain (Ikpikpuk River to Colville River). Alaska Dep. Fish and Game, Fairbanks, Alaska. 54 pp. 212

Bendock, T., and J. Burr. 1985a. Catalog of North Slope lake and stream surveys. Rep. by Alaska Dep. Fish and Game, Fairbanks, Alaska. 33 pp. 137[A]

Bendock, T., and J. Burr. 1985b. Freshwater fish distributions in the central arctic coastal plain (Topagoruk River to Ikpikpuk River). Alaska Dep. Fish and Game, Fairbanks, Alaska. 30 pp. 214

Berg, L. S. 1948–1949. Freshwater fishes of the USSR and adjacent countries [translation]. Zool. Inst. Akad. Nauk. 27, 39, 30. 177[B]

Berg, L. S. 1957. Omul—*Coregonus autumnalis* (Pallas). *In* Commercial fishes of the USSR. Moscow, 1949. 789 pp. [Fish. Res. Board Can., Translation Ser., No. 110. 4 pp.] 178[D]

Bickham, J. W., S. M. Carr, B. G. Hanks, D. W. Burton, and B. J. Gallaway. 1989. Genetic analysis of population variation in the Arctic cisco (*Coregonus autumnalis*) using electrophoretic, flow cytometric, and mitochondrial DNA restriction analyses. Biol. Pap. Univ. Alaska No. 24:112–122. 223

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An Introduction to Anadromous Fishes in the Alaskan Arctic

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Abstract. The arctic environment of western North America imposes a set of harsh physical and biological constraints upon anadromous fishes. These conditions are not unique to the Arctic, but their severity is extreme: (1) arctic aquatic habitats are very cold, with annual averages of only 1°C in coastal waters and 2.5°C in large rivers, (2) winter freezing reduces stream habitat available to fish by some 95 percent, (3) fish must accumulate most of their year's food reserves during the brief 3-month summer period, and (4) densities of fish prey in arctic rivers are very low. Despite these constraints, several salmonid species are well adapted for life in the Arctic, for several reasons. The fish have had over 200,000 years at their present location since Pleistocene glaciation to adjust genetically to the specifics of the arctic environment. Key environmental variables, such as the seasonal availability of food and habitat, fluctuate predictably on an annual cycle, thereby facilitating adaptation to them. The fish are also able, through migration, to select the most favorable conditions available (e.g., warmest water temperatures and the relatively abundant food supply in coastal waters). Further, as K-strategists, the fish are resilient to short-term adversity.

INTRODUCTION

Arctic streams in western North America seem an inhospitable place for fish to live—the streams are cold, they provide little in the way of fish food, and they freeze nearly solid in winter. Yet several fish species complete their life cycles successfully under these demanding conditions. This paper presents an overview of arctic anadromous fishes and their adaptations to several key features of their environment.

The first part of this paper is intended to serve as a brief introduction to the study area and its fish fauna for the papers that follow in this monograph. The taxonomic status of the species and their "anadromous" life history patterns are described. The second and third parts examine commonly held beliefs that arctic fish populations are regulated by the limited availability of overwintering habitats, and that a life history pattern of anadromy allows the fish access to an abundant food supply in the marine environment. Each of these points is intuitively appealing but neither has been scrutinized. The concluding part of the paper brings these and other ideas together in an overview of fish adaptations to the arctic environment.

I have not attempted to give all of the above topics an even treatment. Rather, this paper describes some general characteristics of arctic fishes and their environment and speculates about the implications of these characteristics.

BACKGROUND

Biological and Physical Setting

The geographic region examined is Alaska's North Slope and the western Canadian Arctic, including rivers and coastal waters of the Beaufort and northeastern Chukchi Seas (Fig. 1). This area is bordered to the east by the Tuktoyaktuk Peninsula and to the west by Point Hope, Alaska (Fig. 2). This segment of the Arctic is relatively uniform in terms of geography, oceanography, and fish fauna (Craig and McCart 1975; Craig 1984a,b). The principal fishes inhabiting the region, and their life history patterns, are listed in Table 1.

Stream Environments

Over 200 streams flow into the coastal waters of the Beaufort and northeastern Chukchi Seas. The physical and biological properties of these streams group naturally into three categories of stream size: (1) the Mackenzie River, (2) coastal rivers, and (3) small coastal streams.

The Mackenzie River (4,200 km) is the second largest river system in North America, dwarfing all other streams in the study area (Fig. 1). Peak flows in spring (30,000 m^3/sec) are about 10 times greater than winter flows, but it is especially noteworthy that the Mackenzie River is, with minor exceptions, the only large river in the study area that flows at all in winter.

In summer the discharge of the Mackenzie River is warm and highly turbid, and satellite photos document its extensive influence on the clearer, colder waters of the southeastern Beaufort Sea (Thomson et al. 1986). Sum-

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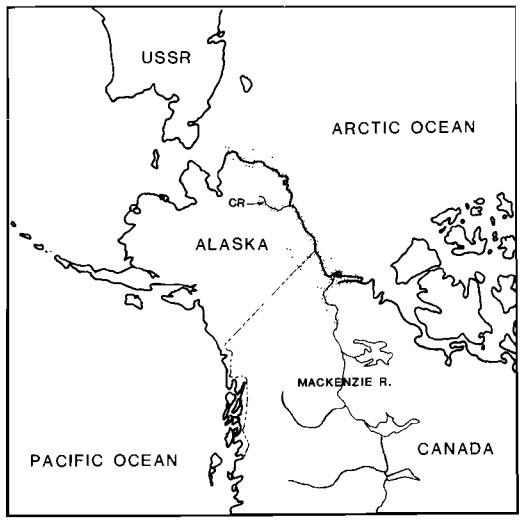

Figure 1. Study area in the western Arctic of North America, showing the two largest drainages, the Mackenzie River followed by the much smaller Colville River (C.R.).

Table 1. Life history patterns of abundant fishes in the study area.

Fish species	Marine resident	Anadromous	Freshwater resident
Arctic cod, *Boreogadus saida*	x		
Arctic flounder, *Liopsetta glacialis*	x		
Fourhorn sculpin, *Myoxocephalus quadricornis*	x		
Pacific herring, *Clupea harengus*	x		
Arctic cisco, *Coregonus autumnalis*		x*	
Arctic char, *Salvelinus alpinus*		x*	
Least cisco, *Coregonus sardinella*		x*	
Broad whitefish, *Coregonus nasus*		x*	
Humpback whitefish, *Coregonus pidschian*		x*	
Lake whitefish, *Coregonus clupeaformis*		x	
Inconnu, *Stenodus leucichthys*		x	
Rainbow smelt, *Osmerus mordax*		x	
Ninespine stickleback, *Pungitius pungitius*		x	
Arctic grayling, *Thymallus arcticus*			x
Round whitefish, *Prosopium cylindraceum*			x
Slimy sculpin, *Cottus cognatus*			x
Northern pike, *Esox lucius*			x
Burbot, *Lota lota*			x

* Key species described in this monograph.

mer water temperatures in the Mackenzie Delta are typically about 15°C, with peaks up to 20–22°C; suspended sediments are generally 200–300 mg/liter, with peaks as high as 1,200 mg/liter (de Graaf and Machniak 1977). Coastal waters off the Mackenzie Delta are stratified, with about 4 m of relatively warm river discharge overlying cold marine water. Some mixing in coastal waters occurs, however, as indicated by variable water temperatures (2–14°C) and salinities (0–31 ppt) from July to September (Lawrence et al. 1984).

The Mackenzie system and adjacent coastal waters support the most abundant and diverse fish fauna in the North American Arctic--some 63 species occur there (Corkum and McCart 1981). The most common fishes in the delta region are (1) anadromous species—Arctic cisco, least cisco, broad whitefish, lake whitefish, Arctic char, and inconnu; (2) freshwater species—lake (trout) char, northern pike, and burbot; and (3) brackish water species—fourhorn sculpin and Arctic flounder. The Mackenzie River is by far the largest overwintering area for stream-dwelling fishes in the North American Arctic.

Approximately 25 other coastal rivers, about 100–300 km long, drain the North Slope. According to the geographic region in which these rivers originate (Fig. 2), they have been called Mountain Streams or Coastal Plain Streams (Craig and McCart 1975). Mountain Streams are prevalent in the eastern portion of the study area, where most originate in the Brooks Range. These streams flow

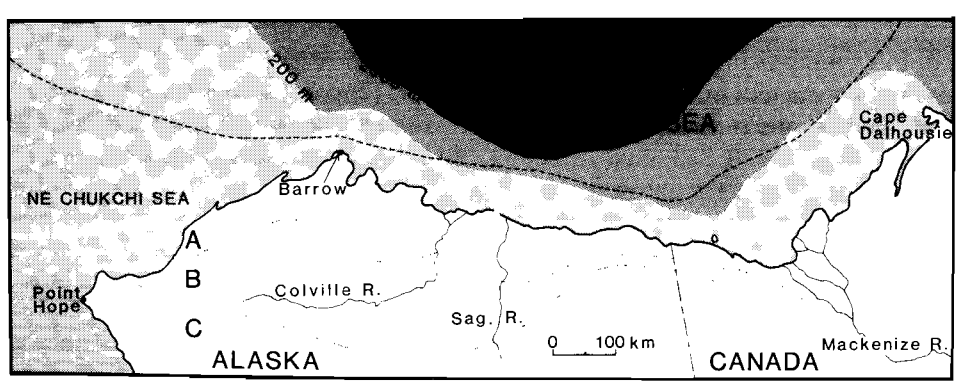

Figure 2. The three physiographic provinces on the North Slope: (A) Coastal Plain, (B) Foothills, and (C) Mountain provinces (after Wahrhaftig 1965 and others), and the average southern extent of the permanent ice pack in summer (dashed line).

for about 6–7 months of the year (late May to about November). Because surface runoff accounts for most flow in Mountain Streams, their annual flow pattern consists of maximum discharge when snow and ice melt during spring breakup (late May or early June), moderate and fluctuating summer flows in response to rainfall (June to early September), decreasing flow in early winter as surface runoff ceases (September to December), and minimal or no flow for the remainder of the winter. These streams freeze to a depth of about 2 m in winter; the few under-ice pools and perennial springs where water does not freeze are used by fish for overwintering. Water temperatures in Mountain Streams seldom exceed 0–1°C in winter and 12°C in summer (maximum about 15°C). The fish fauna of Mountain Streams consists primarily of anadromous Arctic char and several freshwater species such as grayling, round whitefish, and slimy sculpin.

Coastal Plain Streams drain the tundra-covered slopes in the western portion of the study area. Compared to Mountain Streams, these are slightly warmer and slower-moving streams that meander through a network of lakes. Coastal Plain Streams support mainly whitefishes, ciscoes, grayling, burbot, slimy sculpin, and sticklebacks.

Tundra Streams are similar to Coastal Plain Streams except that they are smaller in size and are tributaries to other stream types. The most abundant fish in Tundra Streams is the grayling.

Small streams flowing directly into coastal waters do not support anadromous fish stocks and they provide a negligible contribution to the fish resources of the study area. These small streams, 30–70 km long, depend upon tundra runoff in summer and most freeze solid in winter. Some may support small populations of grayling, slimy sculpin, and ninespine sticklebacks, but most receive little use by anadromous fishes.

Marine Environment

The flat terrain of the North Slope grades gently into the continental shelf of the shallow Beaufort Sea (Fig. 2). The average depth of the shelf is only 37 m, and its width averages 72 km (Sharma 1979). For about 9 months of the year, the shelf waters are covered by ice, with a generally ice-free period extending from late July through September. Major currents are usually westward, driven by the clockwise Beaufort Gyre in offshore waters and by winds in nearshore waters. Fishes inhabiting the offshore portion of the shelf are strictly marine species such as Arctic cod, eelpouts, sculpins, and snailfish (Frost and Lowry 1983).

The nearshore zone is marked by a series of bays, lagoons, deltaic mudflats, and narrow barrier islands. A biologically important feature of the nearshore zone is the occurrence of relatively warm and brackish water (5–10°C, 10–25 ppt) that frequently lies adjacent to the shoreline in summer (Craig 1984a). This estuarine zone extends over much of the length of the coast and is often distinctly different from adjacent marine waters (−1 to 3°C, 27–32 ppt). This nearshore zone provides a transportation corridor for fishes not fully adapted to the marine environment as well as an important feeding habitat for anadromous and marine fishes such as Arctic cisco, least cisco, humpback whitefish, broad whitefish, Arctic char, fourhorn sculpin, and Arctic cod. In winter, the estuarine band is absent, and nearshore waters freeze solid to a depth of about 2 m.

The northeastern Chukchi Sea differs from the Beaufort Sea in several important respects. The source of Chukchi Sea water is the Bering Sea. Bering water flows northward along the Chukchi coastline past Barrow, influencing the Beaufort Sea only slightly. The Chukchi Sea thus forms a transition zone between the Arctic and Pacific Oceans. The fish fauna of the northeastern Chukchi Sea is largely Arctic in its characteristics—it has a low species diversity and a high degree of species overlap (75%) with the Beaufort Sea fauna (Craig 1984b). Marine fishes (Arctic cod, fourhorn sculpin, Arctic flounder, and herring) are abundant in this region, but anadromous fishes are not, for two reasons. First, streams flowing into the northeastern Chukchi Sea are small and produce few fish. Second, the warmer nearshore zone favored by anadromous fishes along the Beaufort coastline is not a characteristic feature of the Chukchi coast—there is less freshwater runoff to establish such a zone and coastal upwelling of cold water against the Chukchi shoreline promotes the exchange of coastal and marine waters more effectively than occurs along the Beaufort Sea.

Terminology: Anadromous vs. Amphidromous

Because this monograph focuses on arctic anadromous fishes, it is perhaps best to discuss the term "anadromous" right at the start. Various definitions have been applied in past years to this and other terms describing fish migrations. Myers (1949) proposed some revisions to this terminology that have received general acceptance for some time:

Diadromous. Truly migratory fishes which migrate between the sea and fresh water:

a. *Anadromous.* Diadromous fishes that spend most of their lives in the sea and migrate to fresh water to spawn (salmon).
b. *Catadromous.* Diadromous fishes that spend most of their lives in fresh water and migrate to the sea to spawn (freshwater eels).
c. *Amphidromous.* Diadromous fishes in which migration from fresh water to the sea, or vice versa, is not for the purpose of spawning, but occurs regularly at some other definite stage of the life cycle.

Using this classification scheme, it is clear that arctic fishes diverge from the definition of "anadromous" in

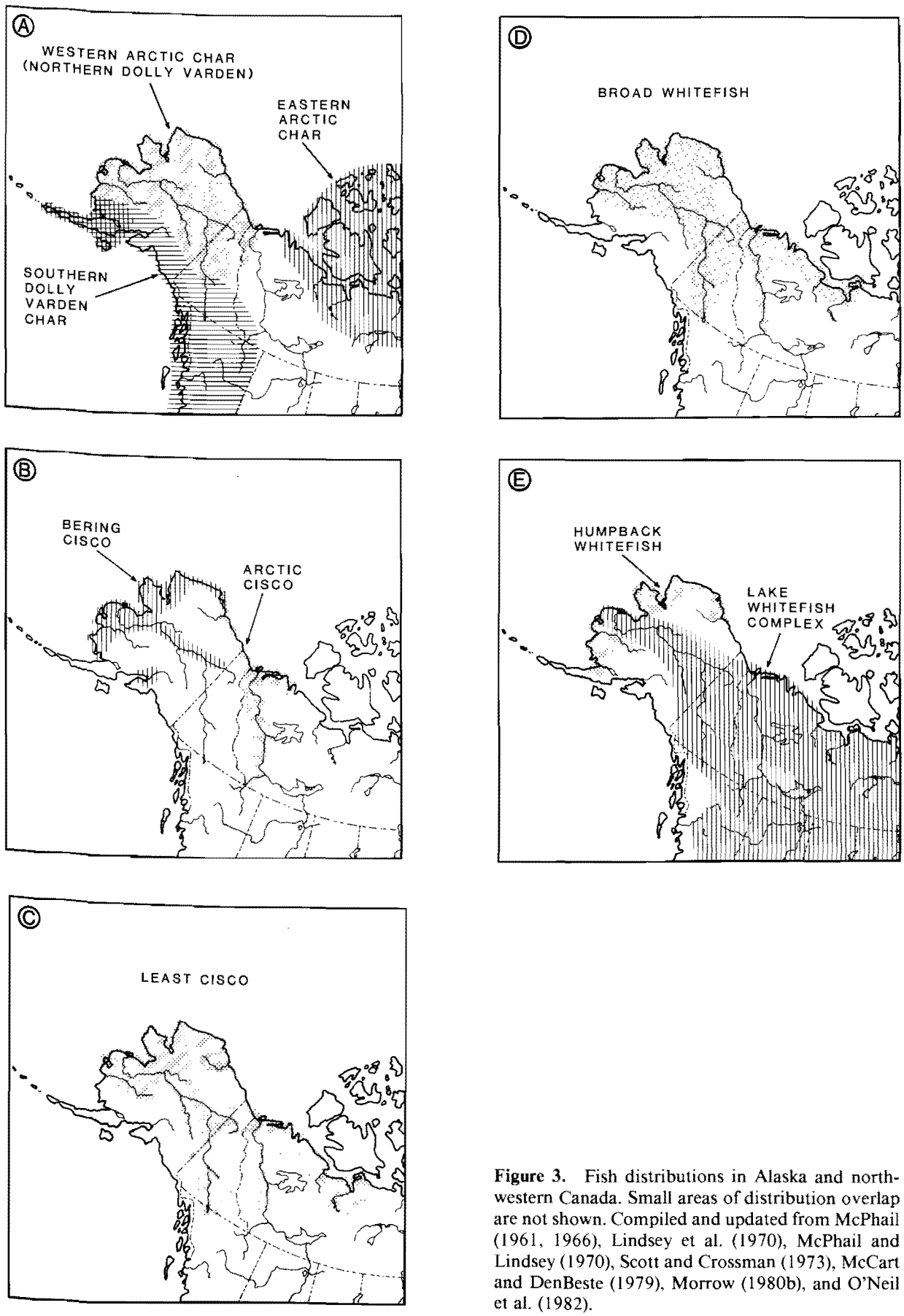

Figure 3. Fish distributions in Alaska and northwestern Canada. Small areas of distribution overlap are not shown. Compiled and updated from McPhail (1961, 1966), Lindsey et al. (1970), McPhail and Lindsey (1970), Scott and Crossman (1973), McCart and DenBeste (1979), Morrow (1980b), and O'Neil et al. (1982).

that they make repeated migrations between the sea and fresh water for other than reproductive purposes, they do not spend most of their lives at sea, and when "at sea" they remain in estuarine coastal waters and generally avoid true marine water. For these reasons, a technically better term for at least some arctic fishes is "amphidromous" or even "estuarine amphidromous" to distinguish these fish from those that migrate into true marine water.

Word meanings are determined by general usage, however, and the current use of "anadromous" has come to mean simply "breeding in fresh water but spending at least part of the life cycle in the ocean" (e.g., Morrow 1980a). Arctic fishes certainly fit this broader definition, and the exclusive use of the term "anadromous" to describe arctic fishes is widespread in the literature, including its use in arctic reference texts by McPhail and Lindsey (1970), Scott and Crossman (1973), Balon (1980), and Morrow (1980a). The term is thus retained in this paper, but the reader should note that the coastal dispersals of arctic fishes are quite unlike the impressive oceanic migrations of salmon.

Fish Taxonomies and North American Distributions

The classifications of chars (genus *Salvelinus*) and whitefishes (genus *Coregonus*) have a history of taxonomic disarray. Their North American populations have often been called "species complexes" that await a better taxonomic resolution, so it is worthwhile to identify the taxonomic uncertainties about the species that are the subjects of this monograph.

One of the more interesting taxonomic controversies concerns the anadromous char in the study area. McPhail (1961) first identified them as the "western form" of the Arctic char *Salvelinus alpinus,* and virtually every field study since then has called them Arctic char. In more recent years, Morrow (1980a) has argued that they are actually the "northern form" of the Dolly Varden char *S. malma.* In either case, taxonomists are probably in agreement on two points: (1) the western Arctic char and the northern Dolly Varden are actually the same fish (Morrow 1980b), and (2) this char differs from both the "true" Arctic char (i.e., the eastern form of *S. alpinus* found in the Canadian High Arctic) and the "true" Dolly Varden (i.e., the southern form of *S. malma* found in the Pacific drainages of southern Alaska) (Fig. 3A).

The problem has been what to call this fish. McCart (1980) and others have retained the name western Arctic char, while Morrow (1980b) and Behnke (1980, 1984) favor northern Dolly Varden. Some consequences of this dual identity are that distribution maps of North Slope char in reference texts reveal an Arctic char bias (McPhail and Lindsey 1970; Scott and Crossman 1973), a Dolly Varden bias (Morrow 1980a), or both (Lee et al. 1980). A recent monograph on the genus *Salvelinus* (Balon 1980) further clouds the issue by describing anadromous char populations on the Alaskan North Slope as *both* Arctic char (Johnson 1980) and Dolly Varden (Armstrong and Morrow 1980).

It is probably premature to consider that this taxonomic issue has been resolved. But the char have to be called something, and so we choose the conservative path and continue to use their established name: (western) Arctic char.

Arctic cisco (*Coregonus autumnalis*) have a more limited distribution than Arctic char (Fig. 3B). Spawning grounds for this species have been located only in the Mackenzie River system, and so it is thought that the Arctic cisco found along the Alaskan Beaufort Sea coastline are of Mackenzie River origin (Gallaway et al. 1983; Bickham et al. 1989). In the western portion of their range, Arctic cisco overlap in distribution with that of the similar-looking Bering cisco (*C. laurettae*). Meristic data from fishes collected in the area of overlap indicate that these are separate species (McPhail 1966; Craig and Haldorson 1981).

Least cisco (*C. sardinella*) are widely distributed in northern Alaska and parts of Canada (Fig. 3C). There are at least two taxonomic forms within this species complex, a nonmigratory form and an anadromous form (McPhail and Lindsey 1970; Mann and McCart 1981). Only the anadromous form is described in this monograph.

Broad whitefish (*C. nasus*) are also widely distributed (Fig. 3D). This is a valid species (Lindsey 1962), and biochemical relationships among arctic populations are currently being studied (J. Reist, Freshwater Institute, Winnipeg, pers. comm.).

The *Coregonus clupeaformis* species complex consists of three forms designated the humpback whitefish *C. pidschian,* the Alaska whitefish *C. nelsoni,* and the lake whitefish *C. clupeaformis* (Lindsey et al. 1970; Morrow 1980a). At least two of these forms occur in the study area (Fig. 3E). The form with low gillraker counts (*C. pidschian*) inhabits the western portion of the study area. In the Mackenzie Delta region, fish have higher but variable gillraker counts indicating that one or both of the other two forms occur there. This problem is currently under investigation (C. Lindsey, University of British Columbia, and J. Reist, Freshwater Institute, Winnipeg, pers. comm.).

Anadromous Life History Patterns

Salmonids are flexible in their life history patterns and exhibit varying degrees of anadromy (Rounsefell 1958; Nordeng 1983). A few species are "obligatory anadromous" in that all members of a population must reside for some time in a marine environment before they can reproduce. In our area the clearest examples of this life history pattern are pink salmon and rainbow smelt, both of which live at sea except to spawn in rivers. Arctic cisco may also be obligatory anadromous, as will be described shortly.

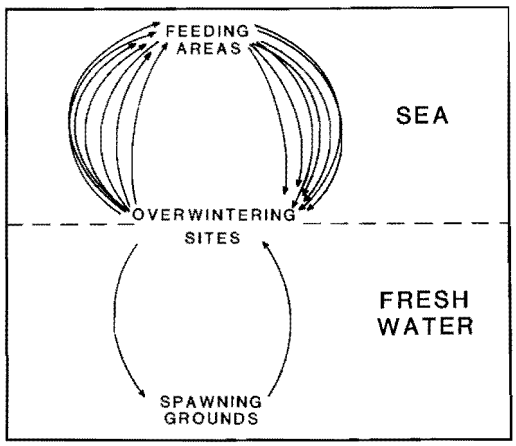

Figure 4. General migration pattern for arctic anadromous fishes, with each pair of arrows to and from an "overwintering site" representing 1 year.

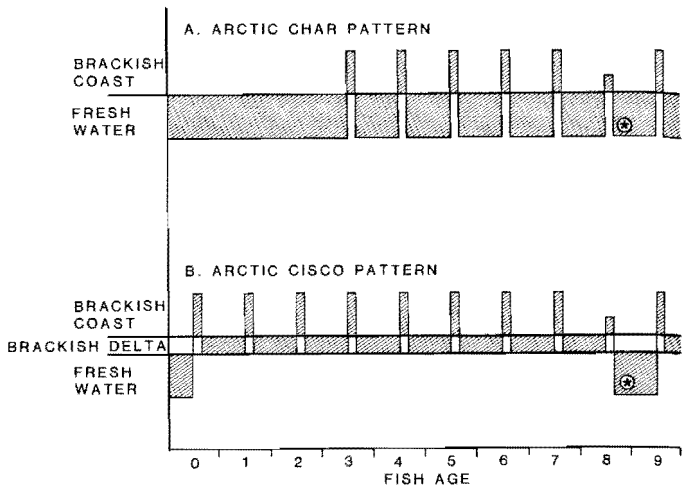

Figure 5. Migration patterns of anadromous fishes between fresh water and the sea, illustrating brief summer migrations to coastal waters and overwintering in fresh water (Arctic char) or brackish water (Arctic cisco). Asterisks indicate spawning in fresh water at age 8.

Other anadromous species (Arctic char, least cisco, and broad and humpback whitefishes) are "facultative anadromous" because all members of a population do not necessarily migrate to sea. For example, some male Arctic char are anadromous while other males in the same population remain in streams for the duration of their lives. These stream-resident males do not attain the large size of sea-run char but they participate nonetheless as "accessory males" in spawning with sea-run females (Bain 1974; McCart 1980). Less is known about the ciscoes and whitefishes but some populations, or members of a population, may also forgo the anadromous habit.

Additional species in the study area may venture from fresh water to coastal waters (e.g., grayling and round whitefish) or vice versa (e.g., fourhorn sculpin and Arctic flounder), but these movements do not represent migrations of diadromous fish as defined earlier. Freshwater fishes may occasionally enter coastal waters when the salinity of the coastal water is low, and marine fishes may enter the lower reaches of rivers, perhaps along with upstream intrusions of brackish coastal waters.

In the study area, the life history patterns of anadromous fishes involve repeated migrations between overwintering sites and coastal waters, followed by a spawning migration into fresh water at maturity (Fig. 4). This cycle consists of three broad phases: spawning, freshwater residency, and anadromy.

Spawning

Char, ciscoes, and whitefishes all spawn in the fall. The spawning period is variable among populations but generally occurs from late August to November, peaking in September and October. These species usually spawn in rivers, but some apparently spawn in lakes as well. These fish do not necessarily die after spawning and some may live long enough to spawn again.

Except for Arctic char, spawning locations are not precisely mapped in the study area. Char spawn in areas associated with perennial springs in or near the Brooks Range in the eastern portion of the study area (McCart 1980). Arctic cisco spawn in the Mackenzie River drainage (O'Neil et al. 1982; Gallaway et al. 1983), and the other species spawn in two general regions—the Mackenzie drainage and the western North Slope region between Barrow and the Sagavanirktok River.

Freshwater Residency

After anadromous fish spawn, their eggs remain in streambed gravels for approximately 7–8 months before the young emerge in spring. The time that these juvenile fish spend in fresh water before smolting is variable within and among species. Based upon fish ages and length frequencies of small fish caught in coastal waters, it appears that Arctic cisco, least cisco, and broad whitefish enter coastal waters for the first time during their first, second, or third summer (ages 0–2) at sizes of 25–200 mm (Craig and Haldorson 1981; Griffiths et al. 1983; Biosonics 1984; Lawrence et al. 1984; Moulton and Fawcett 1984; Envirosphere 1986). Char smolt later—some at ages 1 and 2 but most at ages 3 and 4 (McCart 1980). During their period of freshwater residency, juvenile char inhabit streams, whereas the other species may dwell in either streams or lakes.

Anadromy

Once juvenile fish become anadromous, they enter coastal waters to feed each summer. Two different pat-

terns of anadromy are exemplified by Arctic char and Arctic cisco (Fig. 5):

1. Arctic char pattern. The Arctic char is nearly a freshwater species; it spends little time in the ocean environment. Juveniles often remain in North Slope streams for several years before entering coastal waters for brief periods (about 1.5–2.5 mo) each summer to feed (Fig. 5). Even less time than this is spent in coastal waters during the summer prior to spawning at about age 8. For the "average" char that leads the life indicated in Figure 5, the fish spends only 10 percent of its life "at sea" (i.e., in brackish water), which supports Rounsefell's (1958) findings that Arctic char are among the least anadromous species of the salmonid fishes. Char, then, are more amphidromous than anadromous, as previously discussed.

2. Arctic cisco pattern. Arctic cisco differ from Arctic char in several respects. They smolt at an earlier age, perhaps spend more time in coastal waters each summer (about 2–2.5 mo), and overwinter in brackish water deltas instead of fresh water, at least in Alaska. But like char, they too spawn at about age 8 and may spend less time than usual in coastal waters during the summer prior to spawning. The "average" fish spends about 85 percent of its life "at sea" (i.e., in brackish water) and so Arctic cisco might be better labeled anadromous than amphidromous.

AN ADVANTAGE OF ANADROMY: FOOD

Diadromous migrations of fish can largely be explained by the relative availability of food resources in ocean and freshwater habitats (Gross et al. 1988). Anadromy (rather than catadromy) predominates in temperate latitudes where oceans are more productive than fresh waters. How well does this premise hold for the Arctic?

Is food in Beaufort Sea coastal waters more abundant than in North Slope rivers? This question requires information about (1) the densities of food organisms in different arctic habitats, and (2) the amount or extent of each of these habitats in the arctic environment. Perennial springs, for example, support high densities of benthic invertebrates, but the extent of spring habitat on the North Slope is small, thus moderating the overall contribution of springs as a source of food for fish.

In the calculations that follow, densities of principal prey organisms for anadromous fishes are estimated for coastal waters and three stream categories: Mountain, Tundra/Coastal Plain, and Spring Streams (after Craig and McCart 1975). Two additional aquatic habitats, lakes and offshore coastal waters, are not directly included in this section. Lakes on the North Slope are numerous but many lack channel connections to streams, and in the remaining lakes, the potential sources of food are consumed by freshwater fishes as well as the anadromous ones. The overall contribution of lake food in the diets of anadromous fishes is unknown, but lakes may be particularly important for young-of-the-year fishes, as occurs with Arctic cisco in the Mackenzie Delta (Taylor et al. 1982). Offshore marine waters are excluded because anadromous fish do not range far offshore to feed (Craig 1984a).

Principal Prey

The food habits of anadromous fishes are reasonably well known. In streams, pre-smolt Arctic char feed on aquatic insect larvae, particularly midges (chironomids), caddisflies (trichopterans), and stoneflies (plecopterans) (e.g., McCart et al. 1972; Bain 1974; Glova and McCart 1974; Craig 1977a,b). Adults of these and other insects that fall into the stream are also eaten by char. Diets of pre-smolt ciscoes and whitefishes are not well documented, but some data are available from the Mackenzie River drainage, where juveniles eat chironomid larvae and zooplankton such as ostracods (Hatfield et al. 1972; Jessop et al. 1973; Taylor et al. 1982).

After residing in fresh water for months or a few years, anadromous fishes migrate each summer into coastal waters to feed. The primary foods eaten there are mysids and amphipods, which often account for over 90 percent of their diet; other prey include copepods, fish, and insect larvae (e.g., Craig and Mann 1974; Griffiths et al. 1975, 1977; Bendock 1979; Craig and Haldorson 1981; Bond 1982; Craig et al. 1984; West and Wiswar 1984; Moulton et al. 1985).

From mid-summer to early winter, anadromous fish leave coastal waters and return to streams, lakes, and deltas to overwinter and, when mature, to spawn. The fish generally cease feeding during this fall migration and spawning, but some may resume feeding later in winter (Kogl and Schell 1974; McCart 1980; Craig and Haldorson 1981; Bendock 1981, 1982, 1983). Foods eaten in winter include the previously mentioned insect larvae; large char also consume small fish and fish eggs. Winter food habits of sea-run ciscoes and whitefishes are not well known, but appear to be similar to those of char. In the brackish waters of the Colville Delta, however, overwintering ciscoes and whitefishes consume amphipods, mysids, and fish eggs (Kogl and Schell 1974; Craig and Haldorson 1981).

Prey Densities

To calculate densities of available (and accessible) prey, I examined data pertaining only to the main prey groups eaten by fish—mysids and amphipods in coastal waters, and aquatic insect larvae in streams. There are two sources of the latter group, benthos (organisms living on or in the streambed) and drift (organisms that drift downstream with the current). Studies in arctic streams have shown that the insect larvae eaten by fish are common in both sources (McCart et al. 1972; Craig and McCart 1975; DenBeste and McCart 1984; Glesne and Deschermeir

Table 2. Abundance of fish food in North Slope streams and coastal waters (see Appendix A for details).

Habitat	Accessible fish food (g/m²)*				Habitat surface area (km²)§	Total food in study area (g)*
	Drift	Benthos†	Epibenthos‡	Total		
Spring Streams	0.0002	0.9	—	0.9	1	0.1×10^7
Tundra Streams	0.0006	0.24	—	0.24	296	7.1×10^7
Coastal Plain Streams‖	0.0006	0.24	—	0.24	126	3.0×10^7
Mountain Streams	0.0001	0.1	—	0.1	966	9.7×10^7
Coastal waters	—	—	1.2	1.2	1,500	180×10^7

* All grams are wet weight.
† Assumed to be 10 percent of standing stock.
‡ Assumed to include all mysids plus 50 percent of amphipod standing stock.
§ From Table 5.
‖ Assumed to be similar to Tundra Streams.

1984). Prey were considered to be susceptible to fish predation whether the fish had to move to find the prey (as probably occurs in coastal waters) or the prey moved past the fish (as occurs in streams when a fish feeds on drifting invertebrates); however, when prey groups were not equally susceptible to fish predation, a weighting factor was applied as described below (see Appendix A for details):

Stream benthos. In the eastern region of the study area, Mountain, Spring, and Tundra Streams support very different quantities of stream benthos. Spring Streams support densities of benthic invertebrates that are high even when compared to streams in more southerly latitudes; Tundra Streams have standing crops of benthos similar to those in southern streams; but Mountain Streams are among the most depauperate recorded in the literature. Because char and ciscoes are epibenthic or water-column feeders (rather than benthic infauna feeders), and because benthic invertebrates typically inhabit the spaces between and underneath rocks in the streambed, thus being relatively immune to fish predation, I assumed that only a portion of the benthos, arbitrarily assigned 10 percent, is available to fish predation at any given time.

Stream drift. Invertebrates that temporarily leave the streambed and disperse downstream with the current are an important food source for fish. The few data available indicate, however, that densities of stream drift in the study area are low.

Coastal waters. Major prey species in coastal waters are epibenthic mysids and amphipods. The biomass of these invertebrates in coastal waters is highly variable, ranging between 0.23 and 4.2 g/m² (Appendix A). I assumed that all the mysids were susceptible to fish predation, but only 50 percent of the amphipods because some may burrow into bottom substrates and thus are relatively safe from fish. These calculations are not greatly affected by this assumption because of the comparatively large biomass of mysids present.

A summary of these calculations shows that densities of available prey in coastal waters and Spring Streams are about five times higher than in Tundra and Coastal Plain Streams, which are, in turn, about twice as high as in Mountain Streams (Table 2).

Extent of Each Habitat Type

The surface areas (length × width) of stream and coastal habitats were then calculated to estimate their extent on the North Slope region between Barrow and Herschel Island (details are presented in the following section; Table 5). Coastal waters of the same region are defined as a 750-km-long band of shallow water adjacent to the shoreline, from 0 to 2 km offshore. The width of this zone, 2 km, is a conservative estimate because anadromous fishes will move a few kilometers farther offshore depending on coastal topography, temperature/salinity gradients, etc. (Craig 1984a). Calculated in this manner, the combined surface area of all North Slope streams (1,400 km²) is nearly the same as that of the selected coastal zone (1,500 km²) (Table 2).

Food Abundance in Different Habitats

Although the highest densities of food are found in coastal waters and Spring Streams, coastal waters emerge overwhelmingly as the greatest source of fish food when the surface areas of each specific habitat type are taken into account—not only are prey abundant in coastal waters, but far more of this habitat is available (Table 2). Together, these two features make coastal waters an attractive source of food (Fig. 6).

Spring Streams, despite being rich in benthos, contribute relatively little to the total food supply because of the limited extent of this habitat type on the North Slope. The other stream categories provide only 2–5 percent of the accessible food found in coastal waters, and all streams combined provide only 11 percent of the total food available.

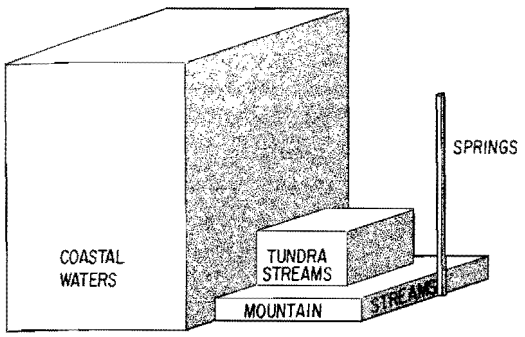

Figure 6. Proportional abundance of food available to fish in aquatic habitats in Beaufort Sea coastal waters and Alaskan North Slope streams. For each box, the length and width indicate the amount of habitat available (i.e., surface area, km^2), and the height indicates the density of food available (g/m^2). Coastal Plain Streams have been combined with Tundra Streams.

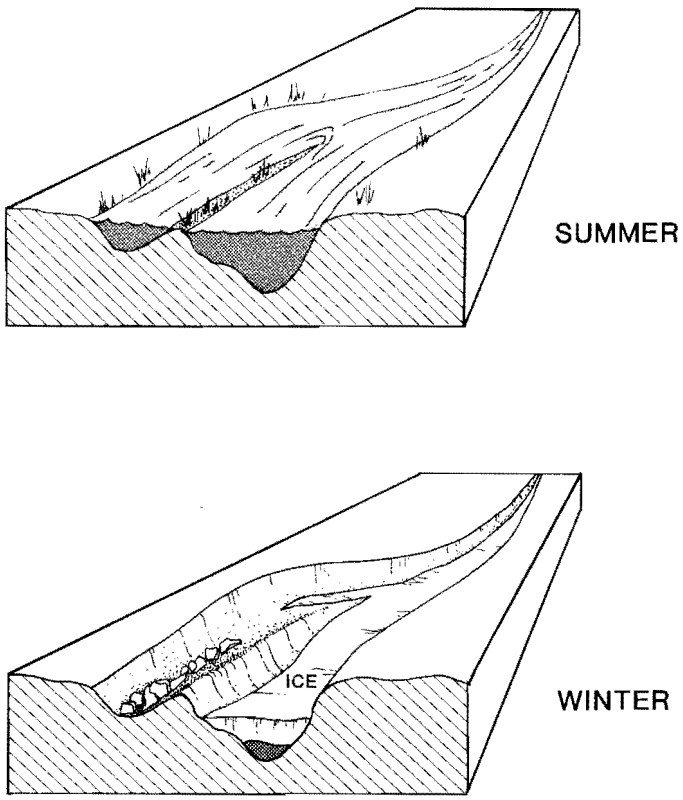

Figure 7. Stream habitat available to fish in summer and winter.

Discussion

For up to three-quarters of the year (the prolonged winter period), feeding by anadromous fishes is greatly curtailed. Reasons for this are varied: (1) fish commonly cease feeding when they migrate from coastal waters to spawning or overwintering areas, (2) cold water temperatures in winter result in a lower metabolic rate among poikilotherms (e.g., fish), hence lower food requirements, and (3) the supply of prey may become depleted in the smaller overwintering areas where fish are concentrated for long periods. Some anadromous fish may resume feeding later in winter, but the overall amount of winter feeding is much less than occurs in summer. It has been demonstrated biochemically that carbon of marine origin is by far the major source of energy for arctic anadromous fishes (Schell 1983; Ziemann 1986).

Only during the brief summer period are anadromous fish able to accumulate the food reserves necessary for growth, reproduction, migration, and winter survival. Virtually all growth of an arctic fish occurs during this period, and a direct relationship between fish size and the onset of sexual maturity is a common characteristic of fishes. But size alone does not assure that a fish will spawn—adults must reach a critical level of food reserves by early summer or they will not spawn during a particular year (Bolotova 1976; Moreau 1983; Dutil 1986). To acquire the necessary food in the short time available, it is clearly advantageous for fish to go where food is most abundant. Furthermore, Nordeng (1983) has demonstrated that a decrease in food availability for young-of-the-year char (in experimental streams) increases the number of fish that become anadromous.

There is evidence that the food supply in coastal waters of the Beaufort Sea is abundant relative to the immediate nutritional requirements of the fish. In Simpson Lagoon (near the Colville River) there was about 50 times more food available than required daily by all vertebrate consumers, including seabirds, whose food needs were much greater than those of fish (Craig et al. 1984). Similarly, predator–prey relationships in Prudhoe Bay indicated that food was generally abundant and not a limiting factor for the anadromous fish there (Moulton et al. 1985).

North Slope streams, on the other hand, produce much less fish food than occurs in coastal waters. Although some of these streams support densities of benthic invertebrates similar to those of streams in the temperate zone, the productivity of arctic streams is much lower due to limited nutrients (Peterson et al. 1985), limited allochthonous input (Cowan and Oswood 1983), and a short growing season. Stream-dwelling invertebrates in the Arctic have relatively long life cycles and thus slow rates of population turnover.

It thus can be concluded that anadromy (amphidromy) confers a strong selective advantage to arctic fishes that are otherwise tied to freshwater habitats for spawning or other activities. Two important caveats, however, are that the coastal source of food is available only for a limited portion of the year, and that there are probably times when even the coastal food supply is low and the fish must then delay reproduction for another year when conditions are more favorable (discussed later).

Table 3. Late winter characteristics of North Slope overwintering areas where fish were actually caught or observed.

Location	Month*	No. sites†	Water depth (m)		Ice depth (m)	
			$\bar{x}$	Range	$\bar{x}$	Range
Spring Streams						
Canning	4	3	0.2	0.1–0.5	0	
Shaviovik	4	1	0.2	0.1–0.5	0	
Sadlerochit sp.	4	1	0.3	0.1–0.3	0	
Fish	4	1	0.1		0	
Firth	4	1	0.5		0	
Anaktuvuk	4	1	0.6	0.3–0.9	0.8	0–2.0
Sag. Tributaries‖	4	4	0.8	0.4–1.2	0.5	0–0.9
Sag. (mid)‖	4	3	0.3	0.2–0.3	2.1	0.6–4.4
Sag. (mid)‖	4	1#	(0.9)#		(2.7)	
Hulahula	4	1	0.3		0	
Mean			0.4			
Deep Pools						
Sag. (mid)‖	3, 5	1	1.4¶	0.9–1.8	2.3¶	2.0–2.7
Sag. (mid)‖	4	1	2.7		1.8	
Sag. (lower)‖	3, 4	3	0.7	0.5–1.0	1.8	1.5–2.3
Sag. (lower)‖	4	1	1.2		2.5	2.1–3.0
Sag. (lower)‖	4, 5	1	2.0		1.7	
Sag. (lower)‖	4, 5	1	2.1		1.7	
Sag. (lower)‖	4, 5	1	1.0		1.7	
Kuparuk (lower)	3, 4	6	1.2	0.5–1.2	1.9	1.7–2.1
Colville (mid)	3, 4	11	2.6	0.6–4.9	1.3	0.9–1.8
Hulahula (mid)	4	1	2.0	1.9–2.1	1.0	0.4–1.5
Mean			1.7		1.8	
Brackish Deltas						
Colville	4	6	6.3	5–7.3	—	
Colville	4, 5	1	—		—	
Colville	5	1	2.7		2.3	

* 3, March; 4, April; 5, May.

† Number of different overwintering sites sampled.

‡ 1, Arctic char; 2, broad whitefish; 3, humpback whitefish; 4, whitefish sp.; 5, Arctic cisco; 6, least cisco; 7, Bering cisco; 8, rainbow smelt; 9, fourhorn sculpin; 10, saffron cod; 11, grayling; 12, lake trout; 13, round whitefish; 14, burbot; 15, slimy sculpin; 16, ninespine stickleback, 17, longnose sucker.

A SEVERE HABITAT CONSTRAINT: OVERWINTERING SITES

Although many factors affect the survival of anadromous fishes on the North Slope, fisheries biologists have long expressed the belief that the availability of suitable overwintering habitat is of paramount importance. In winter, many arctic rivers freeze almost solid, with pockets of unfrozen water occurring only in special areas. Thus, regardless of a river's size in summer, the fish must contend with a much smaller "stream" in winter.

Description of Overwintering Habitats

North Slope streams undergo a profound change in winter, when water gradually stops flowing and the streambeds either dry out or freeze solid throughout much of their drainage (Fig. 7). The freezing process is gradual, beginning in late fall (September) when surface runoff from the drainage basin diminishes. Because the North Slope is underlain by permafrost, the flow of most streams is derived from surface runoff that drains from the shallow "active layer" of unfrozen soil above the permafrost. As winter progresses, this shallow layer and the water in it freeze, thereby terminating the input of surface runoff to streams.

As surface runoff decreases, the water level in streams also decreases, and streams are at their lowest level when they begin to freeze. Where sufficient water is present, the ice thickens to about 2 m (range 1.5–2.5 m) by late winter. The combination of a sharp reduction in water input to streams and the formation of up to 2 m of ice in the remaining water results in the absence of water at most locations. Even the two largest rivers on the Alaskan North Slope, the Colville and the Sagavanirktok, cease to flow

Table 3. Continued.

Diss. oxygen (mg/liter) $\bar{x}$	Diss. oxygen (mg/liter) Range	Temp. °C	Species caught‡	Comments	Reference§
11.5	10–12	1–5	1		1
7.0		2	1		1
10.4		11	1, 11		1
5.0			1	0.1 m^3/sec	2
6.2		2	1	0.4 m^3/sec	2
10.0	8–11	0–1	1, 11–13, 15	0.03 m^3/sec	6
10.0	9–11	0–5	1, 4, 11	All flowing	7
10.0	9–11	0	11, 13–15		8
(<0.2)#		0		Possible fish kill#	8
9.0		−1	1	0.07 m^3/sec	9
8.8					
4.8		0	11, 13		3
3.6		0	14	Isolated pool	8
7	0–15¶	0	2, 3, 11, 13–15		4
9.5	9.2–9.8	0.9	2, 11, 13–15	Isolated pool, no flow	12
13.6	15–16	0	2, 6, 11, 14	Salinity 0.5 ppt	13
1.1	0.3–2.7	0.1	2, 5, 6, 11, 13, 14	Some dead fish, 6.5 ppt	13
5.7		−1.6	5	Salinity 26 ppt	13
11	7–15¶	0	11, 13–16		4
2.3	0.6–5.6	0	2, 11–17	No flow	5
10	9–10.5	0	1	Fish Hole #2	9
6.8					
4.6	2.3–7.8	—	3, 6, 9	Salinity 11–41 ppt	10
—		—	5–10	Salinity 18–32 ppt	11
9.5	4.2–15.0	−0.9	5, 6, 8	Salinity 19–20 ppt	13

§ 1, Ward and Craig 1974; 2, McCart et al. 1974; 3, Alt and Furniss 1976; 4, Bendock 1979; 5, Bendock 1981; 6, Bendock 1982; 7, Bendock 1983; 8, Bendock and Burr 1984a; 9, West and Wiswar 1984; 10, Kogl and Schell 1974; 11, Craig and Haldorson 1981; 12, Dew 1982; 13, Schmidt et al. 1987.

‖ Sagavanirktok River.

Uncertain spring source; site of probable fish kill due to low dissolved oxygen and/or dewatering by industry.

¶ Estimated.

by late winter and freeze to the bottom over long stretches of their course (Arnborg et al. 1966; Childers et al. 1977; Bendock 1981). This severe reduction in unfrozen water increases the importance of the few remaining sites that are available for fish overwintering.

Five types of overwintering habitat have been documented on the Alaskan North Slope (Craig and McCart 1974; Wilson et al. 1977; Bendock 1981, 1982, 1983; Bendock and Burr 1984a):

1. Spring-fed streams and other groundwater sources. Spring Streams are small spring-fed tributaries to larger rivers. Most springs originate along the northern edge of the Brooks Mountain Range. They are generally less than 1.5 km long and 6 m wide, and they have a stable, year-round discharge of about 0.1–1.5 m^3/second (Craig and McCart 1975; Childers et al. 1977). Some springs originate directly within an active channel of a larger river and thus have no separate "Spring Stream" segment.

Because springs flow year-round, they are an important source of unfrozen water in winter. Spring Streams are generally cold (0–5°C), oxygenated (8.8 mg/liter), and shallow (0.4 m deep; Table 3). At the site where they flow into a larger river, there is usually a small ice-free channel about 2–5 km long (Fig. 8). The spring water then continues to flow under ice cover for a variable distance downstream (several hundred meters to a few kilometers) until a barrier to the flow forces the water to the surface, where it freezes and forms a large area of overflow ice. Such areas have been called icings, *Aufeis*, and naleds (e.g., Harden et al. 1977). One of the largest *Aufeis* fields on the North Slope was observed on the Ivishak River; it was 19 km long, 1.5 km wide, and up to 6 m thick (Keller et al. 1961).

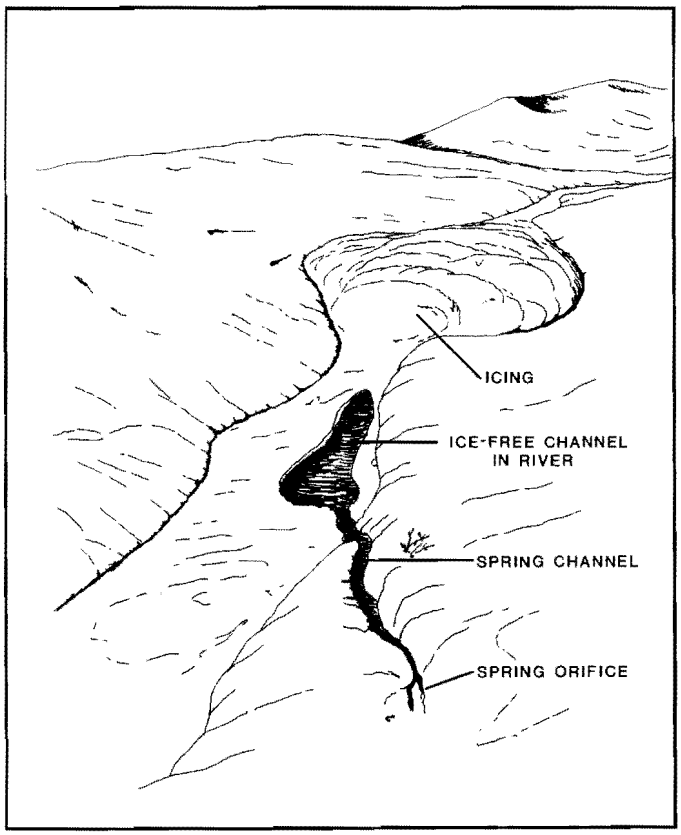

Figure 8. Schematic view of a spring-fed overwintering site.

Bendock (1983) reported that fish can be found throughout the spring area but may be most abundant in the downstream ice-covered section (Fig. 8). Arctic char are known to overwinter primarily in spring-fed areas, but other species have also been caught there: grayling, round whitefish, lake trout, burbot, and slimy sculpin (Bendock 1982, 1983).

2. Deep pools. Under-ice pools of water in the larger rivers serve as winter refugia for fish. The amount of under-ice water is relatively small by late winter, consisting only of a series of pools in the deepest portions of the rivers. These pools are often separated from each other by shallow areas where the ice freezes to the bottom and into the streambed; consequently, flow between pools is negligible—pools that have been drained (by man) apparently do not refill with water (Bendock 1976).

In late winter, 27 under-ice pools containing overwintering fish had an average of 1.7 m of unfrozen water beneath 1.8 m of ice (Table 3). The water in these pools was cold (0°C) and often poorly oxygenated. Low oxygen levels (0.3–2.7 mg/liter) were thought to be responsible for the deaths of fish observed by divers in one under-ice pool in the lower Sagavanirktok Delta (Schmidt et al. 1987).

3. Brackish water deltas. The Colville Delta is unlike other overwintering habitats because of its large size and brackish waters in winter. With channel depths of 2–10 m and a composite channel length of over 70 km, the Colville Delta is second only to the Mackenzie Delta in the amount of potential overwintering habitat on the North Slope. However, unlike the Mackenzie, the Colville ceases to flow in winter, thereby allowing brackish coastal waters to penetrate throughout delta channels (Arnborg et al. 1966; Walker 1974). Winter salinities of 11–40 ppt and even higher have been recorded in this delta (Walker 1972, 1974; Kogl and Schell 1974).

Several species overwinter in the Colville Delta: Arctic cisco, Bering cisco, least cisco, humpback whitefish, broad whitefish, rainbow smelt, saffron cod, and fourhorn sculpin (Kogl and Schell 1974; Craig and Haldorson 1981). In early winter, the whitefishes and ciscoes are the targets of both a subsistence fishery at Nuiqsut and the North Slope's only commercial fishery (Craig 1987).

Brackish waters may also penetrate into other deltas of North Slope rivers, but few examples are available. Brackish intrusions have been documented in the lower Kokolik River near Point Lay (Craig and Schmidt 1985) and in the Sagavanirktok Delta (Schmidt et al. 1987).

4. Lakes. Lakes on the North Slope are numerous, but relatively few are thought to be used for overwintering by anadromous fishes. Many lakes are shallow (less than 2 m) and thus freeze solid in winter, or the lakes lack channel connections to streams and thus are inaccessible to anadromous fishes. The extent to which the remaining lakes are used by overwintering anadromous fishes is not well known because few such lakes have been examined in winter. Anadromous fish have been caught in summer in some lakes deep enough to provide overwintering habitat, such as Teshekpuk Lake (Bendock and Burr 1984b). Other lakes, particularly those on the Coastal Plain between Barrow and the Colville River, probably receive some winter use by anadromous fishes. These lakes form part of an extensive aquatic network with Coastal Plain streams and it seems possible that they play a role in the life history of anadromous species like least cisco. In the Mackenzie Delta, Bond and Erickson (1985) and others have found that some lakes are important overwintering habitat for anadromous whitefishes.

Least and Arctic cisco, humpback and broad whitefish, and Arctic char have been caught in 119 North Slope lakes in summer (Bendock and Burr 1985), but it is not clear whether these represent anadromous or lake-resident stocks. For example, the char populations inhabiting headwater lakes in the Brooks Range are the nonmigratory eastern arctic form of the Arctic char (McPhail 1961; McCart and Craig 1971; Craig 1977a). Similarly, least cisco and humpback whitefish have lake-resident life history forms (e.g., Mann 1974; Alt 1979).

5. Coastal waters. A few of the relative uncommon but truly anadromous species overwinter only in coastal or marine waters. Salmon (pink and chum) and rainbow smelt have an essentially marine life cycle except to enter rivers to spawn.

Table 4. Winter movements of tagged fish which, in most cases, were tagged in fall (September) and relocated in late winter (April).

Location	Fish	*N*	Net displacement* of fish in winter (km) $\bar{x}$	Range	Tag type	Reference
Sagavanirktok River						
Accomplishment Cr.	Char	44	0.5	0–1†	Floy dart	McCart et al. 1972
Misc. tributaries	Char	16	5.3	0–17	Radio	Bendock 1983
Mainstem	Burbot	10	1.8	0–9	Radio	Bendock and Burr 1984a
Colville River						
Anaktuvuk River	Char	12	1.2	0.1–2.6	Radio	Bendock 1982
Canning River						
Mainstem	Char	7	6.5	0–17	Radio	Smith and Glesne 1982
Mainstem	Char	15	10.8	0–20	Radio	Daum et al. 1984
Hulahula River						
Fish Hole #2	Char	8	0.3	0–1.3	Radio	West and Wiswar 1984
Mean			3.8‡			

* Displacement = total distance moved from tagging site to where last relocated.
† Approximation.
‡ Mean of means emphasizes average movement in seven different overwintering areas rather than average movement of 112 individual fish.

Most other anadromous species vacate Alaskan coastal waters in winter and return to rivers, deltas, and lakes to overwinter (Craig 1984a). To date, no ciscoes, whitefishes, or char have been caught overwintering in Alaskan coastal waters, although ciscoes have been caught off the Mackenzie Delta (Bond 1982 and others) and off Siberia (Berg 1957).

Fish Activities in Overwintering Areas

Overwintering areas are often more than places where fish simply reside during the long arctic winter—some species also spawn and feed there.

Anadromous salmonids and coregonids are all fall-spawners whose eggs incubate in streambed gravels throughout the winter. Spawning must occur in an area where a winter water supply is assured. Because such areas are scarce, spawning often occurs in or adjacent to the same areas where the fish overwinter.

The spawning of char in spring-fed areas is well documented (e.g., McCart 1980). Craig (1978) notes that "in the smaller North Slope drainages, which have few areas suitable for fish overwintering, it is conceivable that a single spring-fed site might harbor virtually all members of a particular char population, from eggs in the gravel to adult fish, during the 8–9 month winter period." It is important to note, however, that not all overwintering areas are used for spawning. One of the best known examples of spawning–overwintering segregation occurs in the Sagavanirktok River, where the nonspawning segments of char populations from several tributaries overwinter in a different tributary (the Ivishak River). Spawning sites of the other species are not as well known, but spawning has been documented in deep pools, lakes, and large deltas (e.g., Kogl and Schell 1974; Bendock 1976; McElderry and Craig 1981; Sekerak et al. 1985).

Some fish feeding also occurs in winter. The extent of winter feeding appears to be slight, however, and variable among populations, or at least variable at different times in winter. Among individual stocks of Arctic char, for example, 27–100 percent of stomachs sampled in winter were empty (summarized by McCart 1980).

Confinement of Fish in Overwintering Habitats

Overwintering areas diminish in size as winter progresses and ice thickness increases. By late winter, pockets of unfrozen water are often very localized and bounded both upstream and downstream by shallow areas where the streambed is dry or frozen solid. For example, Accomplishment Creek, a 45-km tributary of the Sagavanirktok River, freezes solid in winter except for a single 2–3-km section of stream where flow is supplied by a perennial spring, and this site is used by Arctic char for spawning and overwintering (Craig and McCart 1974).

As overwintering fish cope with steadily decreasing winter habitat, their movements become more and more restricted. In cases where the movements of tagged fish have been followed through a winter, there was an average net movement of only 3.8 km during the 8-month period from September through April (Table 4). Most of this movement occurred in early winter, when the fish were

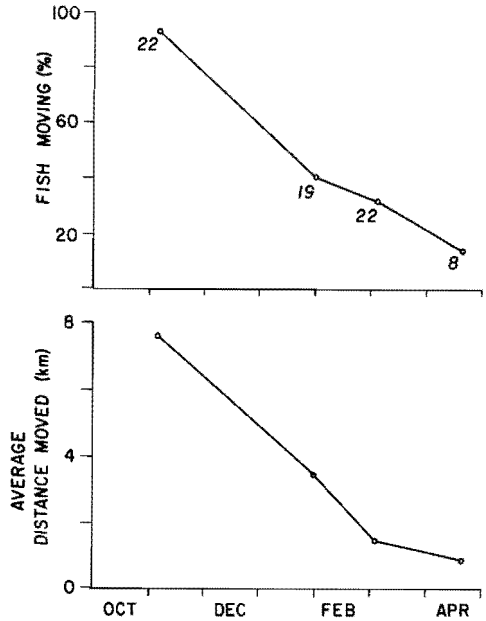

Figure 9. Winter movements of radio-tagged Arctic char (adult nonspawners) in the Canning River. Data from 1981–1982 (Smith and Glesne 1982) and 1982–1983 (Daum et al. 1984) have been combined. Sample sizes are indicated—22 fish were tagged but not all were relocated during every survey. The average distance moved pertains only to relocated fish.

least restricted by ice. As winter progressed both the number of char moving (some not moving could have died) and the distance they moved decreased sharply (Fig. 9).

Loss of Stream Habitat in Winter

To determine the magnitude of habitat reduction in winter, the extent of stream habitat available to North Slope fish in summer and in winter was estimated based on assumptions listed in Appendix B. Values used in these calculations are approximate, but some imprecision can be tolerated because the aim is to estimate the relative proportion of habitat reduction rather than its absolute dimensions. Also, the reduction is so large that the calculations are not overly sensitive to the input variables—almost any variable can be doubled or halved without significantly changing the general conclusion.

Estimates of stream habitat in summer pertain to the North Slope region between Barrow and Herschel Island. Streams in this region were first divided into four stream categories (after Craig and McCart 1975): Mountain Streams, Spring Streams, Tundra Streams, and Coastal Plain Streams. Using 1:1,000,000 topographic maps, I counted the total number of each stream type and measured their lengths with a cartographic map wheel. The sum of their lengths was used as an estimate of the total stream length available to fish in summer (Table 5).

The extent of potential overwintering habitat in each of the above stream types was estimated by first dividing

Table 6. Assumed proportions of stream lengths which provide suitable overwintering habitat for fish (see Appendix B).

Stream type	Potential overwintering habitat in each stream section (%)				Average (%)
	1*	2*	3*	4*	
Spring	100	100	100	100	100
Mountain	10	20	30	40	25
Coastal Plain	0	10	20	30	15
Tundra	0	0	0	5	1

* Each stream sector is 25 percent of the stream length from headwaters (Section 1) to mouth (Section 4).

Table 5. Estimates of North Slope stream dimensions in summer and late winter. *N* = approximate number of streams between Barrow and Herschel Island (see Appendix B for details).

Stream type	*N*	Summer averages				Late winter averages			
		Length (km)	Width (m)*	Total length (km)	Total surface area (km²)	Length (km)†	Width (m)	Total length (km)	Total area (km²)
Mountain Streams	21	210	200	4,410	882	50	25	1,050	26
Tributaries‡	210	20	20	4,200	84	0	0	0	0
Spring Streams	120	2	6§	240	1	2	6	240	1
Tundra Streams	320	45	10§	14,400	144	0.5	5	160	1
Tributaries	2,030	15	5	30,450	152	0	0	0	0
Coastal Plain Streams	7	180	100	1,260	126	30	10	210	2
Totals				54,960	1,389			1,660 (3%)	30 (2%)

* Mid-summer values for the whole stream, from headwaters to mouth.
† Calculated from Table 6.
‡ Steep tributaries in Brooks Mountain Range.
§ From Craig and McCart 1975.

a "representative" stream of each type into four equidistant sections from headwaters to mouth and then assessing the overwintering potential in each section (Table 6). The rationale for these assessments is again provided in Appendix B. Total stream lengths (in summer) were then multiplied by the percentage of each stream type that would provide suitable habitat in winter (from Table 6). In this manner, the total length of each stream type was summed, for a grand total of 54,960 km of stream habitat in summer and 1,660 km in winter (Table 5 and Fig. 10). This ratio represents a 97 percent reduction of stream length available to fish by late winter.

These calculations were taken one step further by comparing the surface areas of streams (average length × average width) in summer and in winter. This step takes two additional factors into consideration: (1) the stream types vary greatly in width, thus measurements of surface area provide a better estimate of total stream habitat available, and (2) the width of a stream is greatly reduced in winter because the shallow portions at stream edges freeze solid. In these calculations, the amount of stream habitat available was reduced by 98 percent in winter (Table 5).

These rough estimates suggest that substantially less than 5 percent of the stream habitat on the North Slope remains available to fish by the end of winter. Similar conclusions were reached in two other North Slope studies—the linear extent of overwintering habitat was estimated as 2 percent of the total lengths of four streams in the Arctic National Wildlife Range (Smith and Glesne 1982), and as 1 percent of the upper Sagavanirktok River (DenBeste and McCart 1984).

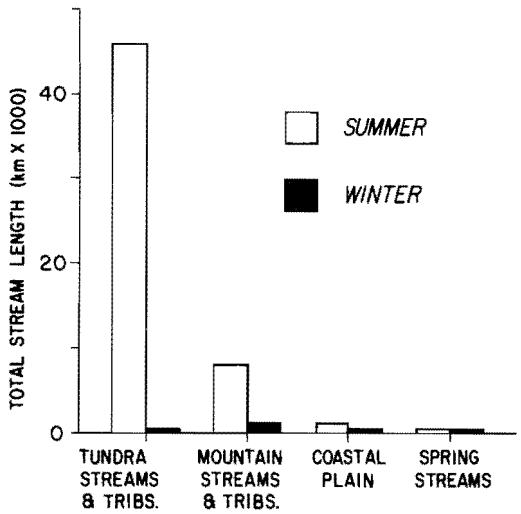

Figure 10. Total lengths of North Slope stream types available to fish in summer and winter.

Discussion

In the realm of environmental impact assessments, overwintering habitats for arctic fishes provide one of the clearest examples of "critical habitat" for animals because (1) overwintering areas are scarce, (2) it is essential that fish use them, and (3) fish in them are captive until spring breakup. All life history stages (from eggs in the gravel to adult fish) may be confined to a small space for up to 8 months of the year. Under these conditions, the fish are particularly vulnerable to disturbance caused naturally (e.g., changes in the quantity or distribution of source water) or by man (e.g., water withdrawal).

The locations of overwintering sites in a drainage may vary somewhat from year to year, depending on, for example, the depth of ice formation in winter. In a regional context, however, overwintering sites are relatively fixed features within a river system. During severe winters, or perhaps even during average winters, unfrozen water will exist only at specific sites (perennial springs and other groundwater sources) or in specific regions where hydrological forces maintain sufficiently deep pools, although the exact locations of these pools may vary as the river course changes from year to year. In an evolutionary sense, the need to find one of these fixed overwintering areas must exert a strong selection pressure on the life cycle of arctic fishes. Fish that fail to find an overwintering area do not get a second chance.

Travel to and selection of an overwintering area must be made by an individual fish relatively early in winter because shallow parts of the stream freeze solid early, thereby preventing access to an overwintering area or escape from sites that will ultimately freeze. We might therefore expect little flexibility in the fall migration patterns of these species. Their destination would need to be precisely defined and the timing of their movements scheduled to account for the earliest possible date that freezing might jeopardize their access to an overwintering area. At the same time, however, completely rigid migratory behavior would deny populations the opportunity to expand their distribution or repopulate streams where a previous population had been eliminated. The price for such dispersal is presumably a high mortality rate for fish that do stray. For example, grayling in the Arctic seem to disperse into all manner of aquatic habitats in summer, and as a consequence, their entrapment or stranding in pools that eventually dry up or freeze is not uncommon (DenBeste and McCart 1984).

Despite the rigid constraints imposed by overwintering areas, migration patterns of arctic fishes can be quite complex. For example, Arctic char in the Sagavanirktok drainage may spawn in one tributary and overwinter in another at different stages in their life cycle. Moreover, a few char that were tagged in one North Slope drainage have been recaptured in another (Craig and McCart 1976). Perhaps these were strays that may or may not have been successful in locating a new overwintering area.

Arctic cisco populations in the Alaskan Beaufort Sea display a different type of exchange between drainages.

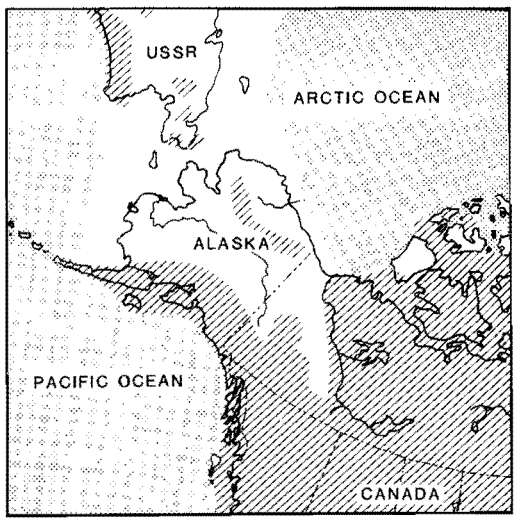

Figure 11. Approximate extent of Pleistocene glaciation during the past 200,000 years (diagonal lines: Illinoian and Wisconsin Periods combined), also showing the Bering Sea land bridge (in white) during glacial periods (after Lindsey and McPhail 1986).

Currently available evidence suggests that a proportion of the Mackenzie River population of Arctic cisco overwinters in the deltas of the Colville and Sagavanirktok Rivers (Gallaway et al. 1983; Schmidt et al. 1987; Bickham et al. 1989). The number of Arctic cisco that do this (estimated by mark–recapture studies to be several million fish) is large enough to support annual harvests of about 60,000 Arctic cisco in combined commercial and subsistence fisheries in the Colville River Delta. From the foregoing line of reasoning about the evolutionary significance of overwintering areas, it cannot be a chance occurrence that so many Arctic cisco overwinter at these particular locations each winter.

If indeed anadromous fish populations on the North Slope are regulated largely by the availability of overwintering habitat, their numbers should be low relative to the large amount of habitat that opens up to them in summer. One study suggests this is the case (although the study deals with grayling, a freshwater species). DenBeste and McCart (1984) found that a large proportion of potentially fish-bearing habitat in arctic streams was "vacant" or underutilized by grayling in summer.

How much summer habitat is "vacant" is not known, but it is unlikely to be as high as 95 percent. Fish in overwintering areas can presumably tolerate some degree of crowding—such tolerance would be adaptive, and at water temperatures near 0°C, the space, oxygen, and food requirements of overwintering fish should be minimal. A study of fish during this 8-month period of confinement would likely improve our understanding of their population dynamics.

ADAPTATIONS TO KEY ENVIRONMENTAL CONDITIONS

The environmental conditions imposed upon fish in the Arctic are not unique to the Arctic, but they are especially severe there. However, there has certainly been enough time for species to adapt to the "hardships of the

Table 7. Adaptations and responses of anadromous fishes to features of the arctic environment.

Environmental condition	Fish adaptation or response
SEASONALLY PREDICTABLE CONDITIONS	
1. Location and seasonal availability of food supply	Obtain year's food supply during the brief summer period and use extra food reserves, if any, for reproduction. Maximize summer intake of food by migrating to the coast where food is most abundant (anadromy)
2. Cold water temperatures	a. "Cold hardiness"—an overall temperature tolerance required for life in a polar environment b. Migratory behavior: in summer, forage in nearshore coastal waters where temperatures are warmest, and in winter, vacate marine environment to avoid extreme low temperatures c. Spawning time: temperature characteristics at spawning site determine when spawning should occur to ensure proper development of eggs in gravel and emergence of fry
3. Habitat reduction in winter	Migratory patterns to ensure winter survival by locating scarce overwintering sites
ANNUALLY UNPREDICTABLE CONDITIONS	
1. Annual variation in food supply	If food supply is too low, skip reproduction for that year
2. Severity of winter affecting size of overwintering habitat	a. Short-term options are minimal; high mortality possible b. Long-term strategy to prevent extinction is to avoid putting all members of a population in the same overwintering site
3. Reproductive success	Increase chances of successful reproduction by outliving "bad" years (K-selection) and having the ability to spawn whenever annual conditions permit (iteroparity)

Arctic." Although the Arctic is considered to be geologically young because of recent Pleistocene glaciation, the North Slope was not glaciated during the last two advances of the glaciers and was instead a refugium for arctic fishes (Fig. 11). Consequently, these species have had more than 200,000 years at their present location to adapt to arctic conditions (and much more time if they inhabited the periphery of earlier glaciers, though at varying sites in North America).

An important factor in determining fish responses to the arctic environment is whether an environmental parameter fluctuates at regular intervals (e.g., seasons) and thus is a predictable event in life cycles, or whether the parameter fluctuates less predictably in time and space. In general terms, arctic fishes have adapted to these conditions in two ways. Seasonally predictable changes are dealt with, in large part, through migration. Annually unpredictable conditions (e.g., factors affecting recruitment of young to fish populations) are dealt with through a life history strategy of K-selection (e.g., long life, repeat spawning), as described below and summarized in Table 7.

Seasonally Predictable Conditions

Availability and Location of Food

One of the most biologically significant aspects of the Arctic is the brief period of biological productivity. With minor exceptions, food is plentiful only during the 3-month summer period (mid-June to mid-September), at which time fish must accomplish most of their annual growth and accumulate food reserves to survive the remainder of the year.

Fish must use this brief feeeding opportunity efficiently by migrating to where food is most abundant. As previously discussed, prey are far more abundant in coastal waters of the Beaufort Sea than in North Slope rivers, which helps to explain why anadromy (amphidromy) is a common life history strategy for arctic fishes.

Habitat Reduction in Winter

One of the most physically significant aspects of the Arctic is the drastic reduction of fish habitat in winter. But this is also a very predictable event in both time and space. It occurs annually, its approach is heralded by obvious environmental cues (cold temperatures, reduced daylight, ice formation), and the under-ice refugia occur each winter at approximately the same locations in the study area. North Slope fish populations have had over 200,000 years to discover the locations of these refugia and to "recognize" the need to occupy them each winter. Adaptations to this temporal and spatial feature of the arctic environment would also be hastened by the annual elimination of all fish that misjudged where to overwinter.

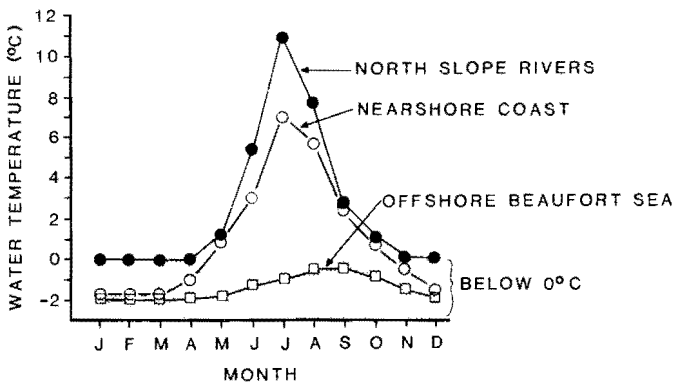

Figure 12. Average monthly temperatures of large North Slope rivers and nearshore coastal waters. Estimated from Griffiths et al. (1975, 1977, 1983), Craig (1977a,b), Aagaard et al. (1981), Craig and Haldorson (1981), Moulton and Fawcett (1984), Craig and Schmidt (1985), Sekerak et al. (1985), and Fissel et al. (1986).

Low Water Temperatures

A cold water regime is also a predictable aspect of arctic aquatic systems. Although some arctic waters briefly warm up to temperatures of 15°C or higher in summer, average monthly temperatures are much lower (Fig. 12). The average annual temperature of unfrozen water is only 2.5°C in large rivers and 1°C in nearshore coastal waters.

Arctic fishes must, in general, be tolerant of such temperatures and have adapted their life history processes to accommodate the effects of low temperatures (as fish have done in cold water habitats elsewhere in the world, e.g., the deep sea). But beyond the genetic "cold hardiness" necessitated by life in a polar climate, the strategy of arctic anadromous fishes seems to be simply to seek the warmest temperatures available in their environment (Fechhelm et al. 1983; Griffiths and Gallaway 1983; Neill et al. 1983; Craig et al. 1985). In summer when these fish forage in Beaufort Sea coastal waters, they generally remain in the nearshore zone where temperatures are usually several degrees higher than in offshore marine waters. In winter, they return to freshwater or brackish habitats, presumably to avoid freezing in the supercooled waters of the marine environment, where temperatures drop to −2°C.

Low temperatures in autumn might cause some anadromous fish to begin moving toward spawning or overwintering areas sooner than appears logical. Bernatchez and Dodson (1985) found that coregonid fishes (cisco and lake whitefish) are not good swimmers compared to most salmonids, and that their swimming performance was much lower, and energy requirements higher, at 5°C than at 12°C. This temperature-related effect may explain the otherwise unaccountably early date that these fish leave coastal waters and migrate upriver. They arrive on their spawning grounds a full 6–10 weeks before spawning starts, having apparently forfeited about half of their summer

feeding period in coastal waters. This would seem to be a "costly energy penalty" compared to fish that had remained in coastal feeding areas until as late as possible and then migrated upstream just in time for spawning. To explain such apparently nonadaptive behavior, Bernatchez and Dodson hypothesized that the effect of low temperatures on the fish's metabolism and swimming performance may necessitate that they migrate upstream before stream temperatures decrease and conditions become energetically less favorable for migration. In our study area, this might apply to Arctic cisco and Arctic char, the two species that have the most distant upstream spawning sites in the study area.

The timing of spawning also reflects the effect of low temperatures. The lower the water temperature, the longer the time required for egg development and emergence of fry. Thus the fish must spawn sufficiently early in fall or winter so that, given the water temperature regime in winter, the fry will emerge in spring at an appropriate time for survival. For those spawning beds that lie directly in the mainstem of large rivers, the timing of fry emergence may be critical because of the dramatic habitat change that occurs at spring breakup. Rivers are then transformed within a week's time from the placid low flows of late winter to raging ice-scoured torrents, which might inflict high mortality on any eggs and pre-emergent fry still remaining in the gravel.

Annually Unpredictable Conditions

Variation in Food Supply

Although a fish can maximize its food consumption by migrating to locations of food abundance, the amount of food available when the fish gets there is not a predictable quantity. In good years the food supply in coastal foraging areas may far exceed the needs of fish for growth and reproduction (Craig et al. 1984), but in bad years it may not. If the fish are unable to build up energy reserves during this period, they will forgo spawning later that year (Bolotova 1976; Reshetnikov 1980; Moreau 1983; Dutil 1986).

Winter Severity

Two aspects of the life cycle of anadromous fishes seem particularly vulnerable to adverse winter weather: overwintering survival and reproductive success.

While the fish have adapted to the scarcity of overwintering sites on the North Slope, the volume of winter habitat actually available to them probably varies from winter to winter. The severity of winter can affect the amount of habitat available to fish in two ways: (1) colder air temperatures, or a lack of an insulative snow cover, can cause an increase in the thickness of ice covering an overwintering site, thereby decreasing the volume of water

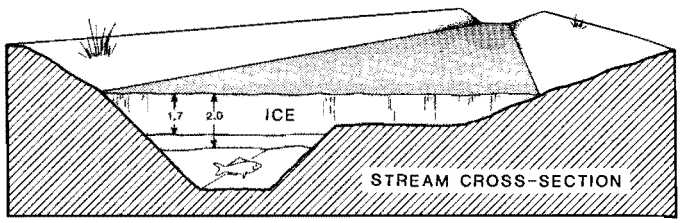

Figure 13. Stream cross-section in winter illustrating a 20 percent reduction in fish overwintering habitat due to a 0.3-m (1-foot) increase in ice thickness.

below, and (2) ice growth may constrict or obstruct stream flow, forcing water to the ice surface, where it freezes as icings, thereby reducing the amount of water flowing to under-ice habitats in downstream areas. It was noted earlier that the average depth of water at known fish overwintering sites was 1.7 m—an increase of only 0.3 m (1 foot) in the thickness of ice covering this "average overwintering site" would decrease its volume of water by at least 20 percent, the exact proportion depending on the shape of the overwintering site (Fig. 13).

In the short term, fish responses to this variation in overwintering habitats are limited because the fish are usually trapped and cannot escape from a continually shrinking overwintering site. It is conceivable that an overwintering site could "fail" altogether, with complete mortality of fishes due to either density-dependent factors (crowding, oxygen depletion) or density-independent factors (cessation of source water, freezing). Such failures may account for the present-day absence of Arctic char at several locations on the North Slope that appear to be suitable overwintering sites (e.g., areas downstream from perennial springs on the Kavik, Katakturuk, and Okerokovik Rivers [Ward and Craig 1974]). Evidence that such mortalities occur in nature is rare because a fish kill under 2 m of ice is difficult to detect in winter and the evidence would be washed out during flooding at spring breakup. However, there are at least three reports of fish kills at overwintering sites—two in the lower Sagavanirktok River (Bendock and Burr 1984a; Schmidt et al. 1987) and one in the upper Dietrich River just south of the study area (Chihuly et al. 1979).

In the long term, at least some fish populations have apparently reduced their chances of extinction by spreading their members over more than one overwintering site, so a catastrophe at any one site would not eliminate all members of the population.

Variability in winter weather may also affect reproductive success. Most anadromous fishes are fall spawners whose eggs remain in the gravel throughout winter and whose young emerge in spring. Adverse weather conditions could cause abnormally high mortalities in two ways: (1) a sever winter might freeze portions of the spawning grounds, or (2) unusually warm or cold waters in winter

might cause the emergence of fry at times adverse to fry survival.

A reproductive failure, through adverse winter weather conditions or a food shortage, would not be particularly catastrophic for arctic fishes. With their long life span and ability to spawn in multiple years, they are able to withstand the loss of an occasional year class.

Discussion

Because arctic fishes, unlike transient "arctic" birds and some mammals, are year-round residents, they have to be physiologically tolerant of arctic conditions during all seasons, although they can seek the most favorable conditions locally available. Life history traits of fish populations also evolve to cope with local environmental conditions. Fish are very flexible in this respect, exhibiting great variation in their life history "strategies."

A life history strategy is a set of coadapted traits designed, by natural selection, to solve particular ecological problems (Stearns 1976). For many species, these traits tend to be associated in two general patterns that have been called r- and K-selection (MacArthur and Wilson 1967; Pianka 1970; and others). Colonizing species are good examples of r-selected populations. They face a high rate of adult mortality each year; to survive over the long run, there must be a high rate of annual recruitment to the population. Individuals in these populations exhibit rapid growth, a short lifespan, and a high annual reproductive effort. In contrast, K-selected populations (e.g., redwood forests) have relatively high survival rates of adults but low survival of eggs or young. Adults are thus long-lived and reproduce enough times so that, despite the low recruitment of young, the population survives.

Arctic anadromous fishes possess unambiguous K-selected traits:

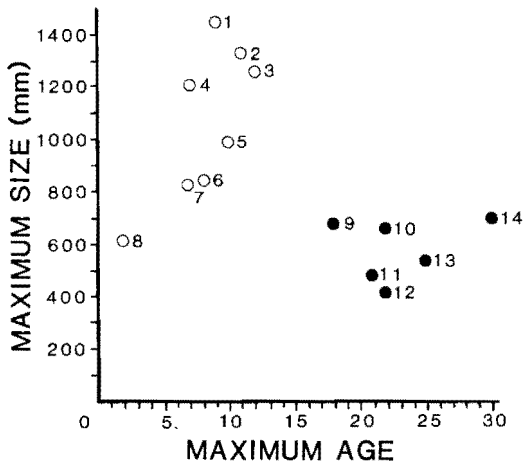

Figure 14. Maximum ages and sizes of anadromous salmonids in the temperate zone (numbers 1–8) and Arctic (9–14): 1, chinook salmon; 2, Atlantic salmon; 3, Dolly Varden char; 4, steelehead trout; 5, cutthroat trout; 6, sockeye salmon; 7, chum salmon; 8, pink salmon; 9, western Arctic char; 10, broad whitefish; 11, Arctic cisco; 12, least cisco; 13, humpback whitefish; and 14, eastern Arctic char. Sources: 1–8, Scott and Crossman (1973); 9–13, Table 8; and 14, Johnson (1980).

1. Longevity. Arctic anadromous fishes have long life spans, with maximum ages of 18–25 years for the five species described in this monograph (Table 8). This contrasts markedly with other anadromous salmonids in temperate latitudes whose maximum recorded ages range from 2 to 12 (Fig. 14).

Longevity is not limited to a small number of individuals—a characteristic feature of arctic fish populations is that many fish live for a long period after becoming mature, so that adult fish comprise a large proportion of the population (Fig. 15). Few fish in the study area, however, live as long as 18–25 years—more representative old ages

Table 8. Maximum and average ages and sizes of anadromous fishes in Beaufort Sea drainages. Parentheses indicate sample size of separate populations. Scale-based ages are not included.

	Age (otolith)			Size (mm)	
Fish species	Maximum	95% Maximum*†	Sexually mature*‡	Maximum	Average maximum*
Arctic char§	18 (14)	10	7 (7)	685 (14)	642
Arctic cisco	21 (5)	10	8 (4)	488 (11)	449
Least cisco	22 (6)	11	7 (4)	414 (12)	359
Broad whitefish	22 (2)	18	11 (1)	655 (8)	563
Humpback whitefish	25 (2)	18	10 (2)	514 (9)	458

Sources. McCart et al. 1972; Yoshihara 1973; Bain 1974; Craig and Mann 1974; Glova and McCart 1974; Mann 1974; Griffiths et al. 1975, 1977; Kendel et al. 1975; Percy 1975; Craig 1977a,b; de Graaf and Machniak 1977; Jones and DenBeste 1978; Bendock 1979; Craig and Haldorson 1981; Bond 1982; Bond and Erickson 1985; Smith and Glesne 1982; Hopky and Ratynski 1983; Daum et al. 1984; West and Wiswar 1984; Sekerak et al. 1985.

* Average of populations, not individuals.

† Excludes the oldest 5 percent of each population.

‡ Age at which 50 percent of a population spawns for the first time.

§ Western arctic form.

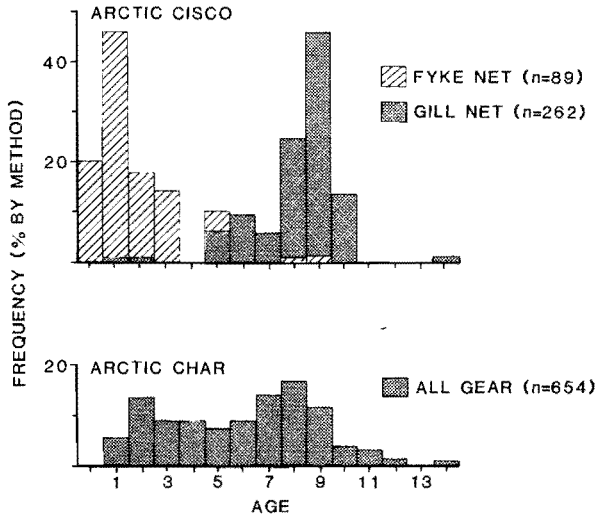

Figure 15. Age frequencies of Arctic cisco and Arctic char in two studies that used a variety of sampling gear, thereby reducing gear selectivity bias for certain sizes of fish: (top) Simpson Lagoon—fyke and gill nets (Craig and Haldorson 1981); (bottom) Canning River mainstem, tributaries, and coastal waters—gill nets, seine, weir, and angling (Craig 1977a).

for these species are 10–18 years if the unusually old fish (arbitrarily designated as the oldest 5% of each population) are excluded from consideration (Table 8).

2. Slow growth. The growth rate of arctic fishes declines markedly once sexual maturity is reached, as is common among fish in general because of the energy demands of reproduction (Roff 1984; J. Craig 1985). Older arctic fish grow only about 1–2 cm each year (Fig. 16).

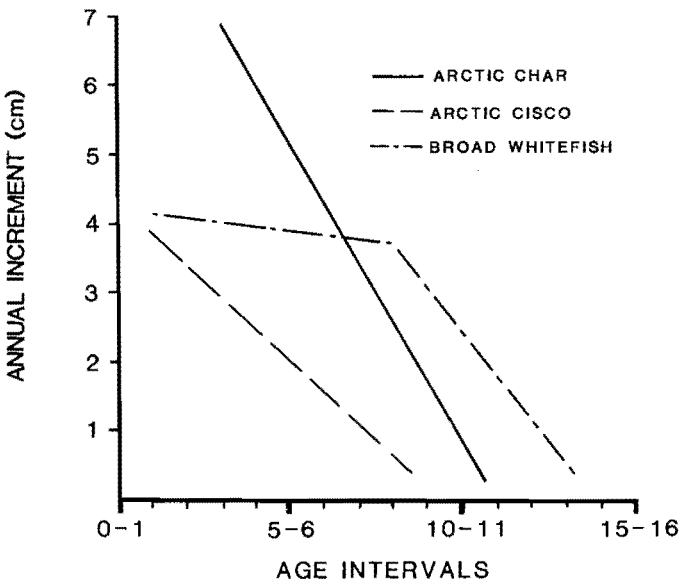

Figure 16. Annual growth increments of anadromous fishes: Arctic char, Canning River (Craig 1977a); Arctic cisco, Simpson Lagoon (Craig and Haldorson 1981); and broad whitefish, Colville Delta (Fawcett et al. 1986).

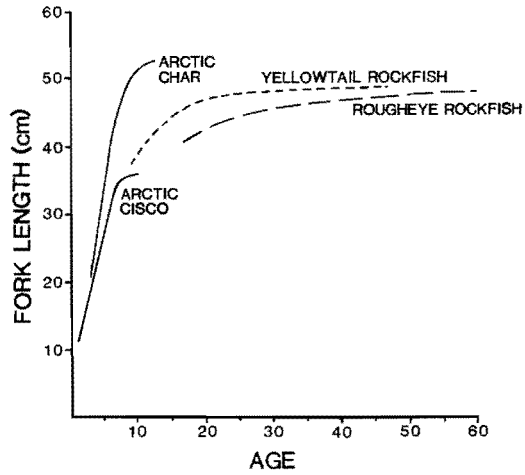

Figure 17. Slow growth rates of arctic fishes compared to rockfishes (genus *Sebastes*) from the Pacific coast of Canada. Sources: Craig (1977a), Craig and Haldorson (1981), and Archibald et al. (1981).

Because of this slow growth rate, maximum sizes of arctic fish are less than those of southern anadromous salmonids, even though arctic fish live much longer (Fig. 14).

3. Delayed maturity. The ages at which half the members of a population spawn for the first time are 7–8 years for char and ciscoes, and 10–11 years for the whitefishes (Table 8). In contrast, the previously mentioned salmonids from temperate latitudes generally mature at ages 2–5 years (Scott and Crossman 1973).

4. Repeat spawning (iteroparity). Arctic anadromous fish do not die immediately after spawning (as do anadromous species such as Pacific salmon). Some live long enough to spawn again, but the frequency of spawning after maturity is probably variable, with some members of a population spawning annually and others at intervals of two or more years, depending on how well the fish fared nutritionally between spawning periods. Char in the Sagavanirktok River, for example, were recaptured as second-time spawners from 1 to 3 years after they first spawned (Furniss 1975). The majority of these recaptures (90%) were taken 2 years after tagging, indicating that char are generally alternate year spawners. Age frequency data indicate that very few of these char lived long enough to spawn a third time. Similar information for the other species is not available.

For perspective, none of the above life history traits is unique to arctic fishes. Rockfishes (*Sebastes* spp.) from coastal waters of the north Pacific Ocean, for example, exhibit K-selected traits that far surpass in magnitude those of arctic fishes. Rockfishes grow extremely slowly and commonly live 40–60 years; some live up to 100 years (Fig. 17).

Nonetheless, arctic anadromous fishes provide clear examples of K-selection, implying that recruitment of their young is, on the average, low. Mechanisms respon-

sible for a generally low recruitment of young could be several, among which are the following:

1. Food supply. Food supply probably plays an important role in the recruitment of young. Because reproduction entails a heavy energy demand, mature arctic fish will not spawn if food is insufficient prior to spawning. A metabolic decision to spawn or not apparently is made months prior to the spawning period, possibly in spring soon after the fish enter coastal waters to feed. Feeding conditions at that time probably influence the number of mature fish that will spawn later that year. In this sense, uncertainty in the food supply at critical times translates into reproductive uncertainty. A poor food year could reduce the requirement of young, not through mortality, but by preventing adults from spawning.

2. Winter mortality. Winter mortality is undoubtedly important in limiting populations, for reasons presented earlier, and mortality may be especially high for young fish. If finding a suitable overwintering site is a learned response for the fish rather than a programmed (genetic) response, many young-of-the-year presumably would be unsuccessful in locating a suitable overwintering site during their first winter. The fortunate survivors, however, could return in subsequent winters to the site in which they successfully overwintered. The net result would be a large loss of young each winter.

3. Other. Two additional factors that could contribute to reduced number of young are (1) predation, and (2) a limited extent of suitable spawning habitat in the study area. There is, however, no dietary information to suggest that predation is a significant problem, and there is no evidence one way or the other regarding spawning habitat.

Although the arctic environment is severe, it does not necessarily follow that fishes lead a precarious existence there. The longevity of arctic fishes attests to their ability to cope with arctic conditions. The K-selection strategy of these fishes also implies something about their population stability. K-selected populations (compared to r-selected populations) are long-lived, have low population turnover rates, and have relatively stable numbers of adults. By having many year classes of older mature fish, they are able to withstand an occasional reproductive loss without jeopardizing the survival of the population.

The topic of stability in arctic fish populations has been examined by Johnson (1981, 1983) and, although his work refers specifically to lake-dwelling populations, his observations are relevant here:

> [lake-dwelling arctic fish] stocks invariably exhibited great age and size, manifesting all the characteristics of continuity and stability in the face of the variable arctic environment. This continuity of the major vertebrate in the ecosystem was in strong contrast with the small mammal stocks of the surrounding terrestrial systems, whose oscillations gave rise to the belief that simple systems are unstable. . . .
>
> The fish stocks in these untouched arctic lakes were recognized as having a structure very similar to that of the dominant tree species in a climax forest (Johnson 1976), giving rise to the conclusion that the lakes in question had also reached a climax, in all significant ways, comparable with the climax of vegetational theory. . . . In both the forest system and the arctic lake, the dominant species is recognizable by its high biomass, large individual size, uniformity in size, considerable age . . . , and a low level of recruitment stock. (Johnson 1981:573)

The Arctic should be viewed, then, as something other than an environment at life's outermost limits for anadromous fishes. Several salmonid species are well adapted for life there. Through physiological adaptations and migration patterns, these species successfully cope with some environmental obstacles, and through their life history strategies, they are resilient to others.

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APPENDIX A. CALCULATIONS OF PREY DENSITIES IN DIFFERENT HABITATS

To calculate prey densities, I examined data pertaining only to the main prey groups eaten by fish—aquatic insect larvae in streams, and mysids and amphipods in coastal waters. When prey groups were not equally susceptible to fish predation, a weighting factor was applied.

1. Stream benthos. Two studies examined 103 stream sites in the eastern portion of the study area and found that Mountain, Spring, and Tundra Streams support very different quantities of stream benthos (Craig and McCart 1975; Glesne and Deschermeir 1984). To estimate the biomass of fish food in each of these stream types, I (1) averaged the biomasses recorded in these two studies, (2) eliminated nonfood items from this total, and (3) used 10 percent of this value as the assumed quantity of benthos actually susceptible to fish predation—this percentage is thought to be an overestimate because most stream invertebrates dwell underneath rocks or within several centimeters of substrate and are thus inaccessible to the fish. More details are presented in Appendix Table 1.

2. Stream drift. Estimates of stream drift in the study area are available for one Spring Stream (Echooka Spring in the Sagavanirktok drainage) and one Tundra Stream (Toolik River in the Kuparuk drainage) (McCart et al. 1972). As indicated in Appendix Table 2, drift densities (no./m^3) were converted to biomass (g/m^3) using average weights of organisms obtained from benthic samples collected at the same sites. Drift in Mountain Streams was estimated using a relationship between stream benthos and drift as described in Appendix Table 2. Because many streams in the study area are less than 1 m deep, the biomass of drift in a cubic meter of water (g/m^3) would actually be spread over several square meters of streambed. Thus, the density of drift over a single square meter is g/m^3 × stream depth. Another way to visualize this constant density of invertebrates drifting past a fish is to consider instead that the fish is swimming through a nonflowing environment with a particular density of accessible food items.

3. Coastal waters. Major prey species in coastal waters are two mysids (*Mysis litoralis, M. relicta*) and several amphipods (*Onisimus glacialis, Pontoporeia affinis, Apherusa glacialis, Gammarus setosus*). These invertebrates may be present throughout the water column, but in shallow coastal lagoons they are 25–200 times more abundant in the region 0–20 cm above bottom substrates than in the entire 2 m of water above (Griffiths and Dillinger 1981). Thus, density units are expressed as g/m^2 of sea bottom (where the prey are) rather than g/m^3 because the fish do not have to swim throughout the water column to find the prey. Densities of epibenthic prey from eight coastal sites or years were averaged (Appendix Table 3). I assumed that all the mysids were susceptible to fish predation, but only 50 percent of the amphipods because some may burrow into bottom substrates and thus be relatively safe from fish.

Appendix A, Table 1. Benthos in arctic streams: estimates of potential fish food.

Stream category	Stream benthos (g/m^2)*		
	Total†	Fish food‡	Accessible fish food§
Spring Streams	12.1	8.7	0.9
Tundra Streams	3.1	2.4	0.24
Mountain Streams	1.1	1.0	0.1

* Wet weight.

† Average of values obtained by Craig and McCart (1975—see Table 4 in 1974 report) and Glesne and Deschermeir (1984: Table 6). Values for the former were 17.0, 4.2, and 1.3 g/m^2 and the latter 7.2, 2.0, and 0.9 g/m^2, respectively, for Spring, Tundra, and Mountain Streams.

‡ Derived from the average proportion of fish prey (Trichoptera, Plecoptera, Ephemeroptera, and Diptera) in total benthos samples from Spring (N = 3 streams, average fish prey 72%), Tundra (N = 4, 79%), and Mountain Streams (N = 5, 89%) (Craig and McCart 1975—see Table 4 in 1974 report).

§ Arbitrarily assumed to be 10% of standing stock of benthos.

Appendix A, Table 2. Invertebrate drift in arctic streams: estimates of potential fish food.

Stream category	Invertebrate drift		Average water depth (m)	Biomass in water column (g/m^2)†
	No./m^3	g/m^3*		
Spring Stream‡	2.5	0.001	0.2	0.0002
Tundra Stream§	2.9	0.003	0.2	0.0006
Mountain Stream	—	0.0001‖	1.0	0.0001

* Based on average weights of similar organisms in benthos (McCart et al. 1972).

† Biomass in water column over 1 m^2 of stream bottom = drift (g/m^3) × water depth (m).

‡ Echooka Spring, average of samples collected in May, July, and August 1971 (McCart et al. 1972).

§ Upper Toolik River, June 1971 (McCart et al. 1972).

‖ Derivation based on relationship between benthos and drift (Elliot 1965; Ulfstrand 1968): $P = (XD)(100)/(Y + YD)$ where P = percentage of benthos in drift, X = drift (organisms/m^2), Y = benthos (organisms/m^2), D = water depth (m). P was estimated as the average value obtained at Echooka Spring on three dates (0.04, 0.10, 0.19%), Toolik River (2.10%), and Lapland Streams (0.01–0.35%, Ulfstrand 1968). Using P = 0.5%, D = 0.3 m where the benthos was measured, and Y = 491 organisms/m^2 (McCart et al. 1972), then X = 0.08 organisms/m^3 = 0.0001 g/m^3.

Appendix A, Table 3. Epibenthic invertebrates in coastal waters of the Beaufort Sea: estimates of potential fish food.

Location	Year	Epibenthic invertebrates (g/m^2)* Mysids	Amphipods	Accessible fish food (g/m^2)†	Reference
Simpson Lagoon	1977	3.1	1.1	3.7	Griffiths and Dillinger 1981:Tables 2, 5, and 22‡
	1978	1.0	0.57	1.3	Griffiths and Dillinger 1981:Table 22 and Figures 12 and 19‡
Prudhoe Bay	1980	0.05	0.18	0.1	Craig and Griffiths 1981:Figures 13 and 14
	1984	0.67	0.70	1.0	Moulton et al. 1985:Figure 4-1
Sag Delta	1982	1.49	0.38	1.7	Griffiths et al. 1983
Harrison Bay	1980	0.37	0.03	0.4	Craig and Griffiths 1981:Table 4
Angun Lagoon	1982	0.41	0.22	0.5	Jewett et al. 1983:Table 4-3
King Point	1980	0.99	0.03	1.0	Griffiths 1981§
Means		1.01	0.33	1.2	

* Wet weight; based on drop net samples as described by Griffiths and Dillinger (1981).

† It is assumed that all mysids, but only half the amphipods, are susceptible to fish predation because some amphipods burrow.

‡ Griffiths and Dillinger 1981: Average values at combined stations and dates were 0.59 (1977) and 0.22 (1978) g ash-free dry weight (A-FDW)/m^2 (their Table 22). These values were converted to wet weight/m^2 using the relationship g A-FDW = 14% wet weight (their Table 5; averaged values for mysids and amphipods); percentage of amphipods in catches were based on their Table 2 (1977) and their Figures 12 and 19 (1978).

§ Density at 6.8-m-deep station.

APPENDIX B. CALCULATIONS OF HABITAT REDUCTION IN WINTER

To calculate the reduction of stream habitat in winter, North Slope streams between Barrow and Herschel Island were first divided into four stream categories (after Craig and McCart 1975): Mountain, Spring, Tundra, and Coastal Plain Streams. In practice, streams were assigned to a category based on the physiographic province in which they originated. Then, using 1:1,000,000 topographic maps and a cartographic map wheel, I counted the total number of each stream type and summed their lengths as an estimate of stream habitat available to fish in summer. Additional details follow:

1. Mountain Streams. These streams were measured as the length of a single channel from the longest headwater tributary to the stream mouth. Multiple channels and other changes in stream width were taken into account in the value used for average stream width in midsummer (200 m). Small headwater tributaries to Mountain Streams were totaled separately because most of these steep creeks receive little fish use in summer and freeze solid in winter.

2. Spring Streams. Although perennial springs are not identified on the maps used, approximately 90 springs have been located in the study area (Craig and McCart 1975; Wilson et al. 1977). I arbitrarily assumed that this represents 75 percent of the springs in the study area, for a total of 120 springs.

3. Tundra Streams. Tundra Streams are the most underrepresented stream category on the maps used because many small Tundra Streams are not shown on 1:1,000,000 maps. A comparison between maps with scales of 1:1,000,000 and 1:250,000 indicated that the former illustrated only half the number of Tundra Streams; therefore, Tundra Streams were increased by a factor of two. Small tributaries to Tundra Streams were totaled separately because these streams dry up or freeze completely and have no overwintering potential. Most small meanders of Tundra Streams and tributaries were not included in estimates of stream lengths because of the difficulty in measuring these on the maps used.

4. Coastal Plain Streams. The main channel of Coastal Plain Streams was measured for this category; the numerous tributaries and interconnections were assigned to Tundra Streams.

The amount of potential overwintering habitat in each stream type was estimated by first dividing each stream type into four equidistant sections from headwaters to mouth and then assessing the overwintering potential in each section (text Table 6); the rationales for these assessments were:

1. Mountain Streams. Headwaters of Mountain Streams are shallow and freeze to bottom substrates except in areas of springs and other groundwater sources. A downstream accumulation of spring water and/or deep holes provide an increasing proportion of overwintering habitat in the lower reaches of the river. The averaged rating of 25 percent overwintering habitat for the complete length of Mountain Streams is thought to be an

underestimate for the largest river in the study area (Colville River) but a reasonable estimate for streams like the Sagavanirktok and Canning Rivers, and it is probably an overestimate for streams in the Arctic National Wildlife Range, where Smith and Glesne (1982) obtained an estimate of only 2 percent potential overwintering habitat in four rivers.

2. Spring Streams. Spring-fed streams are small but flow year-round, thus their averaged rating for overwintering potential is 100 percent of their stream length. Downstream areas where springs flow into other rivers or where springs originate directly within the streambed of another stream type are included in those other stream categories.

3. Tundra Streams. These streams are generally shallow and freeze solid in winter. Perhaps some downstream areas are deep enough to provide a small amount of overwintering habitat. A 5 percent overwintering potential was assigned to their lower reaches, for an averaged rating of 1 percent overwintering potential over the complete length of a Tundra Stream.

4. Coastal Plain Streams. Streams originating on the Coastal Plain have few groundwater sources (Dean 1984) and thus winter flows are probably nil; only deep pools would provide overwintering habitat (Sekerak et al. 1985). These streams were assigned an increasing overwintering potential in downstream reaches, for an averaged rating of 15 percent overwintering potential. Lakes associated with Coastal Plain Streams were not included as potential overwintering habitat in this category.

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Overwintering Biology of Anadromous Fish in the Sagavanirktok River Delta, Alaska

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Abstract. Anadromous fish of the Alaskan Beaufort Sea overwinter for 8–9 months in isolated pools of coastal rivers where free water remains under the ice. Available overwintering habitat represents only about 3 percent of the total water volume available during the short summer. Although current fish impact assessment focuses on summer distribution and abundance, the availability of suitable overwintering habitat may be one of the major limiting factors of anadromous fish populations.

Results of the winter 1985–1986 investigation show that the amount of fish habitat available in the Sagavanirktok River delta is small in comparison to the Colville River delta. Physical and chemical measurements taken during the winter indicate that water quality in terms of life support was generally sufficient; however, marine water intrusions into the Sagavanirktok Delta may cause large-scale avoidance migrations upstream. The resultant crowding at an upstream location was no doubt responsible for near-anoxic conditions and subsequent mortality. Population estimates at this and other locations were calculated from results of diver transects and seine hauls.

The results of length/weight measurements provided a unique insight into the overwintering experience. The broad whitefish population in the Sagavanirktok Delta did little feeding and lost weight, for a given length, as expected. By contrast, the populations of Arctic cisco in the Sagavanirktok and Colville Deltas and least cisco in the Colville had a higher mean body weight at the end of winter. Feeding occurred but the amount of biomass consumed was small and independent of prey availability. Examination of length/weight regressions reveals that mortality may have a profound influence by causing the lighter fish, across the entire length range, to be removed from these populations during the course of the winter.

INTRODUCTION

The extent of overwintering success for anadromous fishes along the eastern Alaskan and western Canadian Beaufort Sea coasts (Fig. 1) has become an important issue as oil and gas development increases in nearshore waters. Overwintering success for any fish species in the Arctic depends on many factors, with two of the most important being the amount of overwintering habitat available and the quality of the habitat in terms of its ability to support fish.

The amount of available overwintering habitat is small compared to the extent of the summer feeding areas, and consequently is of paramount importance. This is particularly true because, as winter progresses, many arctic rivers freeze almost completely solid, leaving only small pockets of unfrozen water in specific areas (Craig 1989).

Results of historical studies have shown that not all anadromous species overwinter in the same habitat type. For example, Arctic char (*Salvelinus alpinus*) are known to spawn and overwinter in habitat associated with perennial springs, typically found in the middle and upper reaches of larger North Slope rivers. Most other anadromous species are found farther downstream in deep pools and deltas of these rivers (Craig and McCart 1974, 1975).

In general, results of late summer sampling in coastal waters of the Beaufort Sea indicate that anadromous species leave these waters by late September to spawn and/or overwinter (Craig and Haldorson 1981; Griffiths and Gallaway 1982; Critchlow 1983; Moulton et al. 1985; Envirosphere 1986). Previous winter fish sampling efforts, conducted between Cape Dalhousie, Northwest Territories, and the Meade River in Alaska, have shown that these species use a variety of overwintering habitats including rivers, delta channels and fronts, and spring areas (Table 1). To date no ciscoes, whitefishes, or char have been caught in the nearshore waters of the Alaskan Beaufort Sea during several extensive winter sampling programs (Craig and Griffiths 1981; Craig and Haldorson 1981). Arctic cisco (*Coregonus autumnalis*), least cisco (*Coregonus sardinella*), and broad whitefish (*Coregonus nasus*) have been found overwintering in and just outside Tuktoyaktuk Harbor, and least cisco have been caught off the Mackenzie Delta (Bond 1982). Thus, not all anadromous species vacate the nearshore waters and move into rivers to overwinter, at least in the vicinity of the Mackenzie Delta. The reasons for these differences are not known, but may be related partially to the fact that the Mackenzie River, unlike other North Slope drainages, continues to flow throughout the winter.

Prior to 1985, most overwintering studies in the Alas-

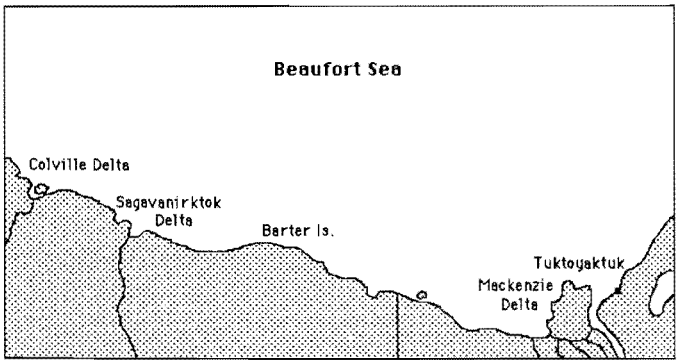

Figure 1. Alaskan and Canadian Beaufort Sea.

kan Beaufort Sea had been conducted upstream of delta areas or in nearshore waters (Alt and Furniss 1976; Bendock 1979a,b, 1981, 1982; Craig and Griffiths 1981; Craig and Haldorson 1981; Dew 1982; Bendock and Burr 1984). The one major exception has been the Colville Delta, which is known to support large populations of overwintering Arctic and least cisco (Craig and Haldorson 1981; Gallaway et al. 1983). Least cisco are also known to spawn in the Colville River, whereas Arctic cisco are thought to represent Canadian migrants from the Mackenzie River. These fish enter Alaskan waters at age 0 or 1, remain for approximately 7 years, and return to the Mackenzie River to spawn at ages 7–9 (Gallaway et al. 1983).

Precipitated by the construction of two extensions to the West Dock Causeway and building of the Endicott Causeway (Fig. 2), the question has been raised whether these structures have blocked the net westward movement of small Arctic cisco. If this is the case, then small Arctic cisco blocked by the causeways may be forced to take up residence in the Sagavanirktok Delta rather than continuing on to the larger Colville Delta. Evidence suggests that Arctic cisco are now and have been winter residents of the Sagavanirktok Delta, at least since the winter of 1981–1982. The presence of small to medium-sized Arctic cisco (120–250 mm fork length) in front of the Sagavanirktok Delta both in 1982 and 1984 and in the vicinity of Howe Island in 1984, prior to any detectable movement eastward from the Colville Delta, suggests that these fish were within the delta at the time of breakup (Griffiths et al. 1983; Moulton et al. 1985). Whether or not Arctic cisco used the lower Sagavanirktok Delta as overwintering habitat prior to 1981 is unknown.

The present study was initiated primarily to investigate two major aspects of fish overwintering habitats: (1) the extent of overwintering habitat available to anadromous and freshwater fishes within the Sagavanirktok Delta, and (2) the quality of overwintering habitat throughout the winter. The specific objectives of this study were to:

1. Identify overwintering areas in the Sagavanirktok Delta;
2. Characterize selected overwintering areas in terms of water quality and prey resources throughout the winter;
3. Determine persistence of fish in the identified overwintering areas;
4. Determine the abundance of fishes in selected areas through the winter;
5. Determine the size/age composition, feeding ecology, and condition of fish found in selected overwintering areas;
6. Make appropriate comparisons with a similar overwintering area in the Colville Delta.

The following abbreviations of fish common names are used: ARCD—Arctic cod (*Boreogadus saida*), ARCS—Arctic cisco, BDWF—broad whitefish, BURB—burbot (*Lota lota*), CHAR—Arctic char, FHSC—fourhorn sculpin (*Myoxocephalus quadricornis*), GRAY—Arctic grayling (*Thymallus arcticus*), HMWF—humpback whitefish (*Coregonus pidschian*), LSCS—least cisco, RBSM—rainbow smelt (*Osmerus mordax*), RDWF—round whitefish (*Prosopium cylindraceum*), SLSC—slimy sculpin (*Cottus cognatus*), SNAL—snailfish species (*Liparis* sp.), and NNST—ninespine stickleback (*Pungitius pungitius*).

STUDY AREA AND METHODS

This study was conducted in the region of the Sagavanirktok and Colville Deltas in the Alaskan Beaufort Sea (Fig. 1). The Sagavanirktok River (Fig. 2) is the second largest river on the Alaskan North Slope; its delta contains two major channels, each of which has several smaller distributaries. The delta is approximately 16 km across and is fronted by several natural islands. Seaward of these islands is a broad (3–4-km), shallow shoal area that, except for channels and isolated holes, is generally less than 1.5 m deep. The Sagavanirktok Delta has been divided by a double breached Y-shaped causeway extending approximately 4.1 km off the coast. The annual flow cycle of the Sagavanirktok River varies from a maximum during spring (early June) runoff to no flow during the winter period. Fish resources of the Sagavanirktok River include both anadromous species (e.g., Arctic char and several species of whitefish) and freshwater species (e.g., Arctic grayling and round whitefish).

An additional sampling program was conducted in the Colville Delta, the terminus of the largest river on the Alaskan North Slope, located approximately 85 km west of the Sagavanirktok River (Figs. 1, 2). The Colville Delta is about 30 km across and has two major channels and numerous minor ones. The flow cycle for this river is similar to that of the Sagavanirktok River. Fish communities for this river are also similar, with the addition of least cisco and humpback whitefish.

Fish and invertebrate sampling was conducted at sites chosen to represent a variety of habitats, including freshwater riverine, and inner- and outer-deltas within the

Sagavanirktok River delta. These sites were examined in November and from these, five were chosen for intensive sampling: three were in the west channel of the Sagavanirktok Delta, one was seaward of Heald Point, and one was near the western tip of the Endicott Causeway (Fig. 2). No intensive sampling stations were located in the east channel of the delta because water depths (generally less than 2 m) in this area appeared less favorable for overwintering. In addition, two stations were located on the westward side of each of the Endicott Causeway breaches during the mid-winter sampling period to determine fish use of the scour zones that formed in the breaches during summer 1985.

The five Sagavanirktok Delta stations and one in the Colville Delta were sampled for fish and prey resources, and physical measurements were taken during each of three sampling periods:

Period 1: 8–24 November 1985
Period 2: 27 February–16 March 1986
Period 3: 24 April–10 May 1986

Under-Ice Fishing Techniques

During each sampling period, several sizes and types of nets were used. Nets were deployed under the ice with a radiolocated jigger board, a Murphy stick, or divers depending upon ice thickness, water depth, and size of the overwintering area to be sampled.

Gill Nets

Three different gill nets were used: (1) a monofilament experimental net 22.9 × 1.8 m (75 × 6 ft) with three equal-sized panels of 25-, 51-, and 76-mm (1-, 2-, and 3-in) stretched mesh; (2) a 15.2 × 1.8-m (50 × 6-ft) braided nylon net with 19-mm (0.75-in) stretched mesh; and (3) a 15.2 × 1.8-m (50 × 6-ft) braided nylon net with 15.9-mm (0.63-in) stretched mesh. All gill nets were sinking nets; however, due to shallowness at most stations the entire water column was sampled. Nets were set for approximately 24 hours, but the sampling effort was abbreviated if catches were high. All fish caught were frozen at the capture site and retained. Gill nets were deployed at Stations 1, 2, 3, 5, and C1 during Period 1; at Stations 1, 2, 3, 6, 7, and C1 during Period 2; and at Stations 1, 2, 6, 7, and C1 during Period 3 (Fig. 2).

Under-Ice Fyke Nets

During the first sampling period, an under-ice fyke net was deployed at Stations 3, 5, and C1 (Fig. 2). The trap was 1.2 × 1.2 × 0.9 m (4 × 4 × 3 ft) deep with four 15.2 × 1.2-m (50 × 4-ft) wings. The trap and wings were constructed of 6.4-mm (0.25-in) knotless nylon mesh and weighted to rest on the bottom. Due to low catch, this method was not used during subsequent sampling periods.

Under-Ice Seine Net

During Periods 2 and 3, a seine was deployed and towed under the ice at lower Sagavanirktok Delta Stations 6 and 7. This net was a 9.2 × 1.8-m (30 × 6-ft) bag seine constructed with 6.4-mm (0.25-in) knotless nylon mesh. The foot rope was weighted with lead rollers and the first 2.4 m (8 ft) of warp line was constructed of galvanized chain to keep the seine on the bottom. This net was pulled manually along a measured path of about 23 m (75 ft) by means of two warp lines extending from the net, along the bottom, and through two holes in the ice. After the seine had been hauled 14 m (45 ft), it was pursed and pulled out a single large hole. This scheme provided a sampling area of about 126 m^2 (Fig. 3). The fish were then hand-dipped out of the bag and either retained or enumerated and released. The net was reset by pulling two lines at the opposite end of the large hole.

Invertebrate Sampling

One drop-net sample for determining the level of epibenthic invertebrate prey organisms (e.g., mysids and amphipods) was usually collected each day when a station was being fished. The drop-net, similar in design to that used by Griffiths and Dillinger (1981), was 0.5 m in diameter (area sampled 0.2 m^2) with a 1.5-m conical net constructed of 1.0-mm mesh netting. A removable sample bucket with identical mesh was attached to the end of the net. Samples were labelled and frozen. Drop-net sampling was done prior to other activities (e.g., checking net or diving) that might disturb the bottom.

One infaunal invertebrate sample was taken with a Ponar sampler at each site fished during each sampling period. The hand-operated Ponar grab sampled an area of 0.05 m^2 to a depth of about 10 cm. The contents of each grab were washed into a large catch bucket, transferred to labelled sample bags, and frozen.

Physical Measurements

Temperature, salinity, and dissolved oxygen measurements were recorded at each station on each sampling day. Measurements were taken at the surface (the underside of the ice) and through the water column at 1-m intervals. Temperature and salinity were measured with a YSI Model 33 S-C-T meter that was calibrated against a Bureau of Standards mercury thermometer and a distilled water blank. Additional field checks of salinity calibration were made with an AO optical refractometer. Dissolved oxygen levels were measured using a YSI Model 57 DO meter. This meter was calibrated daily and the

Table 1. List of previous overwintering studies conducted between the Meade River, Alaska, and the Tuktoyaktuk Peninsula, Northwest Territories.

Location	Date	Gear type	Diss. oxygen (ppm)	Mean temp. (°C)	Mean salinity (ppt)	Fish caught	Reference
Tuktoyaktuk Harbour	1/80	GN*	—	—	—	3 BDWF	Bond 1982
	6/80					107 ARCS	
Kugmallit Bay	3/81	GN	—	—	—	15 LSCS	Bond 1982
Mackenzie Delta							
Swimming Point	3/74	GN	—	—	—	1 HMWF	Percy 1975
Hendrickson Island	3/74	GN	—	—	0.2	1 LSCS	Percy 1975
Harry Ch.	3/74	GN	—	—	—	1 HMWF	Percy 1975
Mallik Bay	3/74	GN	—	—	6.4	25 LSCS	Percy 1975
						1 ARCS	
						1 BDWF	
Moose Channel	10/74	GN	—	1.0	<1.0	4 LSCS	Mann 1975
						1 GRAY	
	11/74	GN	11.8	0.0	<1.0	2 HMWF	
						2 BDWF	
Unnamed lake	11/74	GN	11.6	0.0	<1.0	4 HMWF	Mann 1975
						1 LSCS	
Unnamed lake	11/74	GN	11.8	0.0	<1.0	8 HMWF	Mann 1975
Unnamed lake	4/75	GN	7.4	0.0	<1.0	1 HMWF	Mann 1975
						1 LSCS	
Middle Ch.	4/75	GN	12.4	0.0	<1.0	1 HMWF	Mann 1975
						1 LSCS	
Middle Ch.	10/75	GN	—	3.0	<1.0	3 LSCS	Mann 1975
Middle Ch.	11/75	GN	11.2	0.0	<1.0	1 LSCS	Mann 1975
East Ch.	4/75	GN	—	0.0	<1.0	3 HMWF	Mann 1975
Unnamed lake	11/74	GN	11.0	1.0	<1.0	4 LSCS	Mann 1975
East Ch.	10/74	GN	—	1.0	<1.0	3 LSCS	Mann 1975
						1 BDWF	
Yukon and Alaskan streams							
Firth R.†	4/73	GN	6.2	2.0	0.0	CHAR	McCart et al. 1974
Hulahula R.†	4/83	GN	9.0	−1.0	0.0	CHAR	West and Wiswar 1984
Sadlerochit River†	4/73	GN	10.4	11.0	0.0	CHAR	Ward and Craig 1974
						GRAY	
Canning R.†	4/73	GN	11.5	2.5	0.0	CHAR	Ward and Craig 1974
Shaviovik R.†	4/73	GN	7.0	2.0	0.0	CHAR	Ward and Craig 1974
Sagavanirktok Delta							
Mid-river	4/7?	—	4.8	0.0	0.0	RDWF	Alt and Furniss 1976
						GRAY	
Mid-river springs†	4/83	—	10.0	0.0	0.0	GRAY	Bendock and Burr 1984
						RDWF	
Mid-river springs†	4/83	—	<0.2	0.0	0.0	—	Bendock and Burr 1984‡
Mid-river deep pools	4/83	—	3.6	0.0	0.0	BURB	Bendock and Burr 1984
Lower river deep pools	4/76	—	7.0	0.0	0.0	BDWF	Bendock and Burr 1984
						HMWF	
						RDWF	
						GRAY	
Lower river deep pools	4/82	GN	9.5	0.9	0.0	BDWF	Dew 1982
						GRAY	
						RDWF	
Upper delta	11/85	GN	—	−0.5	0.0	14 BDWF	Enviroshpere 1986
						1 GRAY	

Table 1. Continued.

Location	Date	Gear type	Diss. oxygen (ppm)	Mean temp. (°C)	Mean salinity (ppt)	Fish caught	Reference
Mid-delta	11/85	GN	—	0.0	5.0	32 BDWF 14 RDWF 6 ARCS 4 GRAY	Envirosphere 1986
Lower Delta	11/85	GN	—	−0.5	20.0	60 ARCS 1 LSCS 1 BDWF 1 RDWF	Envirosphere 1986
Kuparuk R.	4/76	GN	11.0	0.0	0.0	GRAY RDWF	Bendock 1979a
Colville River							
Deep pools Anaktuvuk R. Ninuluk Cr.	4/79 3/80	GN	2.3	0.0	0.0	GRAY BDWF RDWF	Bendock 1981
Deep pools Umiat Bar Prince Cr.	10/77 4/78	GN	2.2	1.0	0.0	GRAY BDWF RDWF	Bendock 1979b
Anaktuvuk R.	4/81	GN	10.0	0.5	0.0	CHAR GRAY RDWF	Bendock 1982
Colville D.	4/73	GN	4.2	—	13.0	LSCS HMWF	Kogl and Schell 1974
Colville D.	4/78	GN	—	—	—	69 ARCS 44 LSCS 5 BRCS	Craig and Haldorson 1981
Meade R.	11/83	GN	—	—	—	87 LSCS 22 HMWF	Sekerak et al. 1985

* Gill net.
† Spring-fed streams.
‡ Suspected natural fish kill due to low oxygen levels.

probe kept warm prior to use to prevent freezing the membrane.

Under-Ice Diving Techniques

Scuba divers were used to deploy under-ice nets, conduct visual transects to census fish, determine dimensions of available overwintering area, and operate underwater video equipment during the second and third sampling periods at Stations 1, 6, and 7. During Period 2 divers were also employed at Stations 8 and 9.

Diver-estimated fish densities were determined by swimming a series of transects radiating out from the center of the dive hole. Transect lengths were measured from meter markings on the safety line, and transect widths were estimated by the diver and were a function of water clarity. Along each transect line the diver counted the number of each of the most abundant species of fish observed within his field of view and reported these counts to the tender upon surfacing. Each transect from the same dive hole was considered a replicate sample with the assumption that there was little or no lateral movement of the fish between transects. These replicates were used to calculate a mean density, which was then applied to the measured dimension of the overwintering area to yield a population estimate for each species in the overwintering hole.

During Period 1, a self-contained VHS mini-cam and lighting system mounted in an underwater housing was used at Stations 1 and 3. The mini-cam housing was connected to a 2.4-m stainless steel pole that allowed the unit to be lowered through a hole in the ice. This unit was then rotated through 360 degrees at various depths for the duration of the battery life (approximately 20 min). Recorded tapes were reviewed at the end of the day. This technique was employed in an effort to detect the presence of fish at the survey sampling sites. This method of stationary video recording was discontinued during later

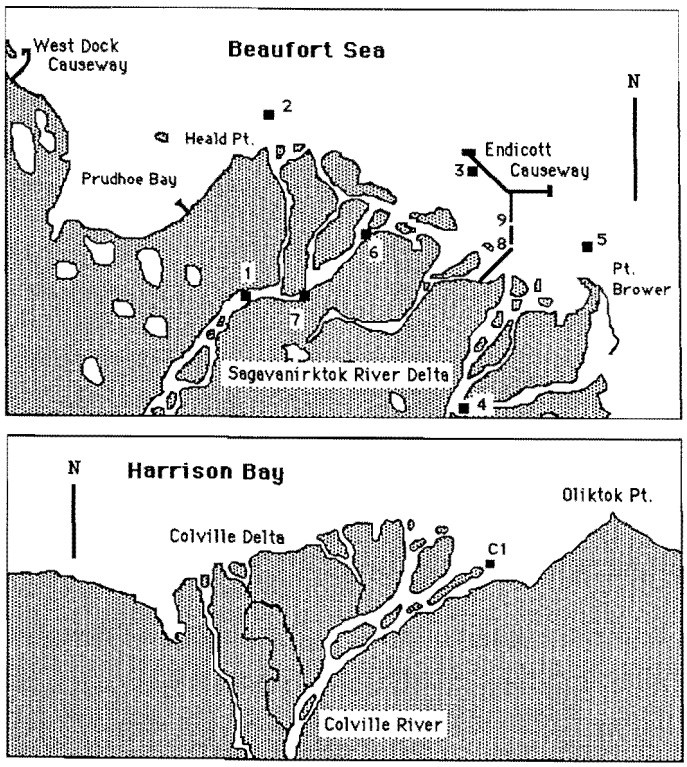

Figure 2. The Sagavanirktok and Colville Delta study areas illustrating sample locations.

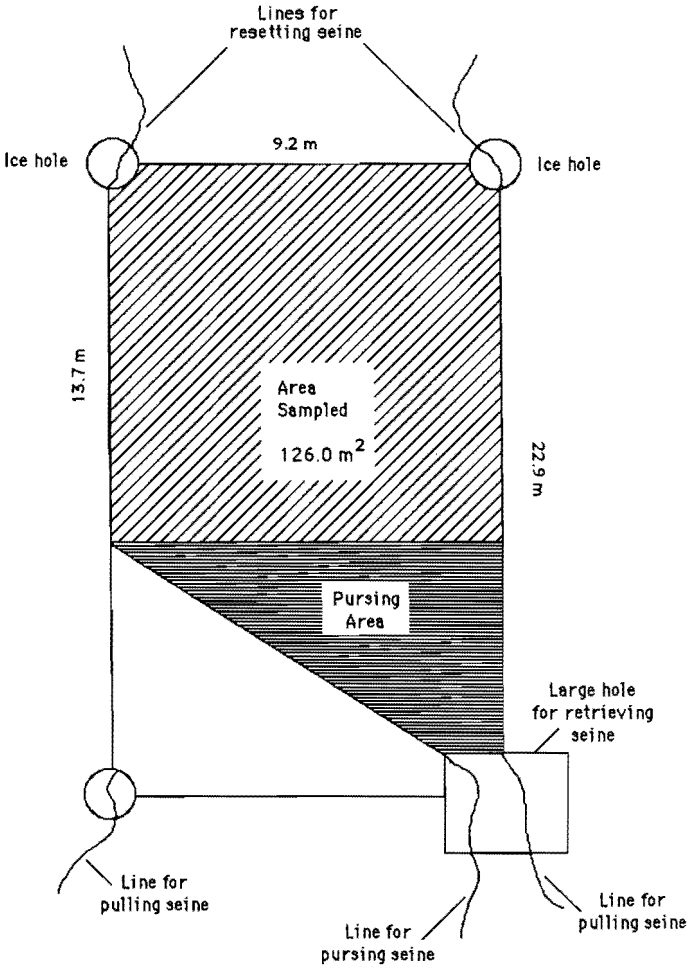

Figure 3. Schematic representation of under-ice seine nets.

sampling periods because of the limited area surveyed by a fixed-position camera assembly.

In an effort to make the video camera mobile, divers were used during the last two sampling periods. Station 8 (a breach in the causeway; Fig. 2), which was too confined to string a gill net, was surveyed during Period 2, and Station 7 was surveyed during Period 3. The latter survey was helpful in documenting high fish densities and the presence of dead fish.

Fish and Invertebrate Sample Processing

At the end of each sampling period, frozen fish specimens were thawed and dissected. The following data were recorded: fork length (nearest 1 mm), egg diameter (nearest 0.1 mm), body weight and gonad weight (nearest 1 g), and state of maturity.

Fish stomachs that contained food were preserved for later analyses. In the laboratory, each stomach sample was weighed (to the nearest gram). Prey species were identified to major taxonomic groups, except mysids, which were identified to species. Each taxon was enumerated and wet weighed using either a Mettler PE 160 (0.001–160 g) or a Mettler 451 (0.0001–160 g) analytical balance. In addition, mysids were measured for total length. When the amount of a given taxon was large, total count and weight were estimated by placing the entire sample into a square dish sectioned into 36 equal-sized cells, counting and weighing the organisms contained in four cells, and extrapolating the results by multiplying the counts and weights by 9 (36/4).

Fish Aging

Otoliths were removed during fish dissection and placed in vials containing glycerine. Fish ages were estimated by analysis of the otoliths according to the criteria and methods of Nordeng (1961) and Williams and Bedford (1974). Two independent readings were made of each otolith, and in cases where age determinations differed, a third aging was made. If a consensus was not reached, then the otolith was excluded from further analysis.

For age determination of older Arctic cisco, an otolith from a young-of-the-year fish was used to provide a reference starting point against which counts were made. This technique helped to establish the position and characteristics of the first annulus. Because of the similarity in otolith growing patterns between both species of cisco, otoliths from young-of-the-year Arctic cisco were also used to establish the first annulus of least cisco. The otoliths from a cohort of 2-year-old broad whitefish were used as a reference for aging older members of this species.

Otoliths from older fish were aged using a lateral surface reading of an intact otolith. If annuli were difficult to distinguish, the otolith was broken in half, scorched with an alcohol flame, and examined under a dissecting microscope (7–30 power) using high intensity side lighting to enhance surficial detail. By convention, 1 January has been used as a fish's birthday; however, fish captured during Period 1 (November) were aged as if they had been caught after the first of the year so that results from all three periods could be combined.

RESULTS

Physical Conditions

Physical measurements (temperature, salinity, and dissolved oxygen) were typically taken throughout the water column at 1-m intervals at each active netting station and prior to each diving or netting effort. The results for early, mid-, and late winter are presented below for five stations that represent the various habitat types encountered during the study and include: (1) the freshwater Station 1 in the upper Sagavanirktok River delta, (2) the brackish-water Station 7 in the middle Sagavanirktok Delta, (3) the marine Station 6 in the lower Sagavanirktok Delta, (4) the marine Station 2 offshore of Heald Point, and (5) the Colville Delta, Station C1. Mean values for these stations are presented in Figure 4.

Water temperatures in overwintering areas were consistently at or near the freezing point for the ambient salinity throughout the winter. The coldest temperatures therefore occurred at the stations with the highest salinities (Fig. 4). Salinities at Station 1 remained low (0.4–1.3 ppt) during the winter, indicating that marine water intrusion into the Sagavanirktok River delta did not penetrate this far upstream. Slightly brackish conditions (5–6 ppt) at Station 7 (approximately 3 km downstream of Station 1 land 12 km upstream from the coast) indicated that this station was near the upper limit of marine intrusion. At Station 6, average salinities increased from 20 ppt to about 28 ppt between Periods 1 and 2. These results indicate that marine water had already moved up the western channel of the Sagavanirktok River by mid-November and that this process continued into February and March. By Period 2, physical conditions at this lower delta station were similar to those at the outer delta Station 2 (Fig. 4). At the Colville Delta station, average salinities ranged from 15 to 22 ppt, and thus showed increases similar to those found at Station 6 in the Sagavanirktok Delta. It was clear that marine waters moved into the Colville Delta during winter, but possibly due to the larger volume of fresh water in this delta at the start of freezeup, salinities did not reach marine levels.

As freezeup begins, the flow of water from arctic rivers diminishes and eventually ceases. A wedge of marine or brackish water then starts to move upstream. The upstream extent of the salinity wedge is variable, ranging from 30 to 40 km in the Colville River (Kogl and Schell 1974) to approximately 12 km in the Sagavanirktok River (Dew 1982; Bendock and Burr 1984; Envirosphere 1986; this study). The differences are probably due to the greater portions of the Sagavanirktok River that are frozen to the bottom, which may restrict the upstream movement of marine or brackish water.

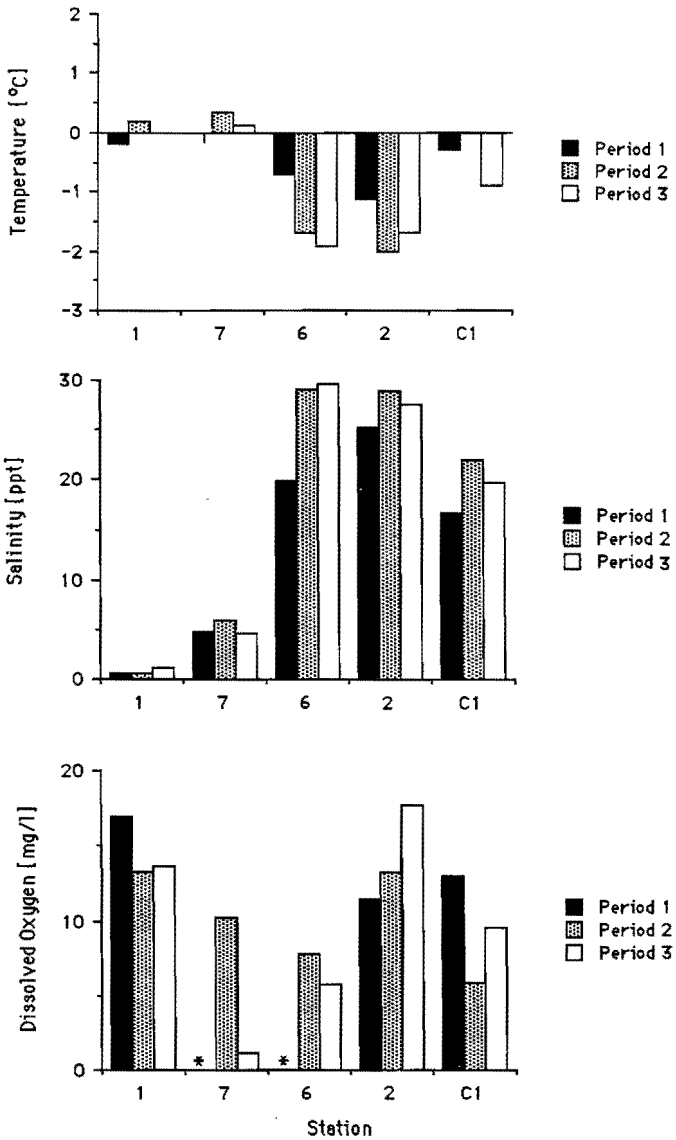

Figure 4. Mean physical data (temperature, salinity, and dissolved oxygen) collected at each station–period combination at stations in the Sagavanirktok and Colville Deltas. Values are means from all depths sampled. *Indicates no data collected.

Dissolved oxygen levels were greater than 5 mg/liter at all station–date combinations sampled throughout the winter, with the major exception of Station 7 during Period 3, when levels fell to a mean of 1.1 mg/liter (Fig. 4). The causes of this decrease are not known, but are probably related to the large number of fish in this pool and its decreasing size as winter progressed (see "Winter

Table 2. Species composition and numbers of fish sampled in the Sagavanirktok and Colville Deltas during the winter of 1985–1986. Numbers are pooled counts from all gill nets, fyke nets, seines, and diver observations.

		Sagavanirktok Delta						Colville Delta		
		Station 1 (fresh water): Period			Brackish and marine stations: Period			Station C1 (brackish): Period		
Species	Code	1	2	3	1*	2†	3‡	1	2	3
Arctic cisco	ARCS	0	0	0	0	126	178	144	14	8
Least cisco	LSCS	0	0	1	0	1	4	62	23	14
Broad whitefish	BDWF	12	49	122	0	29	52	0	0	0
Humpback whitefish	HMWF	0	0	0	0	0	0	2	0	0
Round whitefish	RDWF	1	2	9	0	3	21	0	0	0
Arctic grayling	GRAY	18	51	27	0	10	94	0	0	0
Rainbow smelt	RBSM	0	0	0	0	1	0	8	7	2
Fourhorn sculpin	FHSC	0	0	0	3	234	0	19	1	0
Slimy sculpin	SLSC	0	0	0	1	0	0	0	0	0
Arctic cod	ARCD	0	0	0	0	8	0	0	0	0
Burbot	BURB	0	2	5	0	2	6	0	0	0
Snailfish	SNAL	0	0	0	8	2	0	0	0	0
Ninespine stickleback	NNST	0	0	0	0	5	0	0	0	0
Total		31	104	164	12	421	355	235	45	24
Grand Total										1,391

* Stations 2, 3, and 5.
† Stations 2, 3, 6, 7, 8, and 9.
‡ Stations 2, 6, and 7.

Abundance of Fish" section below). Bendock and Burr (1984) also reported low dissolved oxygen levels (<0.2 ppm) at a station in the mid-reaches of the Sagavanirktok River and associated it with a natural winter kill of fish, possibly due to overcrowding.

Species Composition

Sampling stations in the Sagavanirktok Delta covered a wide range of habitats extending from freshwater to near-marine conditions, whereas the Colville Delta station remained relatively brackish throughout the study (salinity range 20–24 ppt). Thirteen species of fish, totaling 1,391 individuals, were caught or observed by divers (Table 2). Of these, 62 percent were anadromous species (Arctic and least cisco, broad and humpback whitefish, and rainbow smelt), 19 percent were freshwater species (round whitefish, grayling, slimy sculpin, burbot, and ninespine stickleback), and 20 percent were marine species (fourhorn sculpin, Arctic cod, and snailfish).

Arctic and least cisco were found only in brackish water, with the exception of a single least cisco caught at Station 1 during Period 3. Broad whitefish were most abundant at freshwater Station 1 in the Sagavanirktok River and were absent from the Colville Delta collections. The latter observation was somewhat surprising, because broad whitefish are known to spawn in this drainage, and the presence of brackish water would not appear to be a deterrent given that they were found at Station 7 in the Sagavanirktok Delta. These results suggested that Arctic and least cisco and broad whitefish are able to remain in brackish water throughout the winter, although broad whitefish seem to prefer fresher water. The few humpback whitefish and rainbow smelt caught in the Colville Delta were also in the brackish water.

Freshwater fish were also caught in brackish water, most at Station 7, where salinities ranged from 5.8 to 6.7 ppt. This was the farthest upstream intrusion of brackish water and was separated from upstream freshwater areas by a wide, shallow section in the river that had frozen to the bottom by mid-November.

The three marine species documented during this study (fourhorn sculpin, Arctic cod, and snailfish) were found only at brackish-water stations, primarily the coastal stations (2, 3, 8, and 9). The largest concentration recorded by divers was over 50 sculpin observed at Stations 8 and 9. These stations were located at deep pits associated with breaches in the Endicott Causeway.

Winter Abundance of Fish

During the winter of 1985–1986 there was a general decrease in fish abundance as reflected in catch-per-unit-effort (CPUE) of gill nets (Fig. 5) at all sampling sites except Station 7. The most striking example occurred with Arctic cisco at Station 6. During Period 1, the CPUE for large individuals was relatively high (2.61; calculated from Envirosphere 1986) and this value dropped sharply

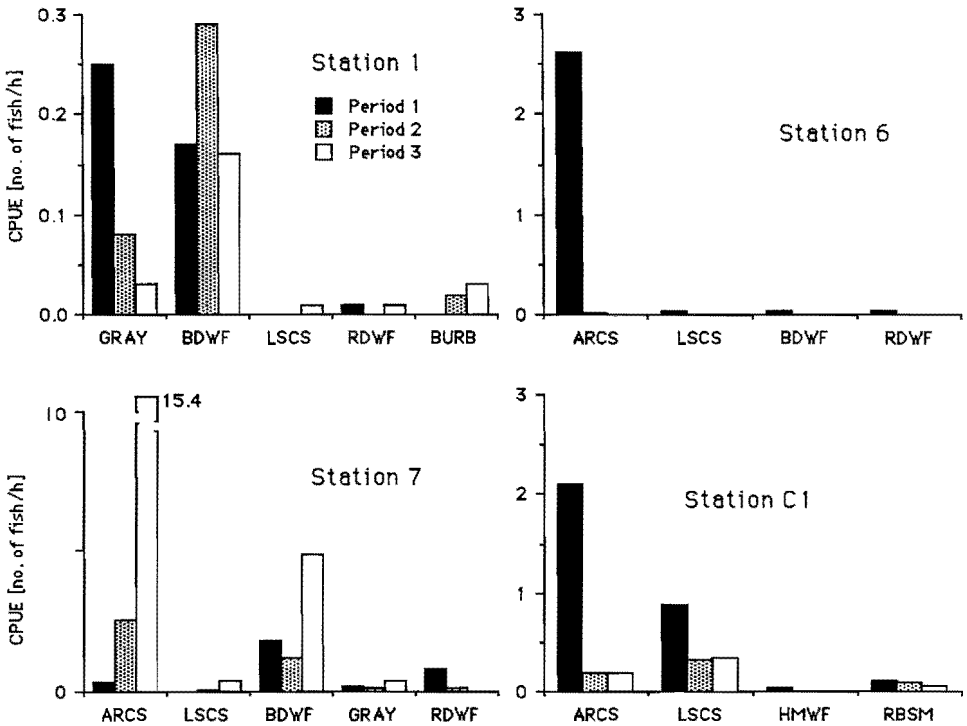

Figure 5. Catch-per-unit-effort (fish/hour) of the major fish species gillnetted at Sagavanirktok and Colville Delta Stations 1, 6, 7, and C1 during each sampling period in winter 1985–1986.

to near zero during Periods 2 and 3. This decrease coincided with increased salinities from 19.8 to 29.0 ppt (Fig. 4). Diver transects conducted during Periods 2 and 3 confirmed the absence of large Arctic cisco at this station (Table 2). Thus, increasing salinities in the lower delta during this period may have forced the fish to move upstream to areas with less saline waters. This process may also have been partially responsible for one of the major trends in seasonal CPUE: the sharp increase of Arctic cisco CPUE after Period 1 at Station 7 from a low of 0.32 to 2.40 and 15.38 for Periods 2 and 3, respectively (Fig. 5). This increase probably occurred relatively early in the winter, when there was still a contiguous water mass extending from Station 6 to 7. Later in winter, surveys indicated that the river froze completely in this area, thus isolating upstream areas from a further intrusion of brackish water. Access to overwinter sites farther upstream (e.g., Station 1) was also blocked by ice.

Catches for the three major species, Arctic and least cisco and rainbow smelt, at the Colville River station were highest during Period 1 (Fig. 5). This corresponds to the time when the Colville commercial fishery operates (J. Helmericks, pers. comm.). Subsequent catches in the mid- and late winter were substantially lower for all three species. The reasons for the late season decreases are not known, but may reflect a movement of fish to less saline overwintering areas. Such a pattern could also result from fish becoming less active and thus less likely to be caught in gill nets or other passive gear.

Population Estimates from Diver Transects and Seine Hauls

Population estimates based on mean densities and the total volume of each overwintering pool (from Envirosphere 1986) are given for Stations 1, 6, and 7 in Tables 3–5. It should be noted that the volume of the overwintering pools often decreased between Periods 2 and 3 due to increases in ice thickness.

At Station 1, the population estimates for broad and round whitefish and burbot were similar between the two sampling periods (Table 3), suggesting that these fish remained in the general vicinity for most of the winter. The population estimate at Station 1 for grayling decreased from 303 in Period 2 to 40 in Period 3. The reasons for this decline are not clear, but several explanations are possible. Grayling may have either moved out of the Station 1 area altogether or distributed themselves within the pool differently. The latter seems a reasonable explanation because (1) surveys upstream from Station 1 during Period 1 showed water depths were sufficiently shallow to be frozen solid by mid-winter, and (2) water quality measurements at Station 7, 3.2 km downstream, indicated separate water masses (see "Physical Conditions" section). In addition, grayling appeared to be distributed more evenly during Period 3 (count range 1–6 for eight transects) than during Period 2 (count range 2–24 for five transects). This suggests that the population estimate for Period 2 may have been biased upward. It is unlikely that

Table 3. Population estimates for fish species observed at Station 1 during Periods 2 and 3.

Species	Mean density (no./100 m³)	Estimated volume of over-wintering area (100 m³)	Estimated population no.
Period 2			
GRAY	7.58	40	303
BDWF	6.21	40	248
RDWF	0.46	40	18
BURB	0.16	40	6
Period 3			
GRAY	0.99	40	40
BDWF	4.29	40	172
RDWF	0.28	40	11
BURB	0.13	40	5

natural mortality was responsible for the decrease because water quality measurements indicated good overwintering habitat during both periods, and no dead fish were observed by divers during either sampling period. Gillnet mortality was also unlikely because only six grayling were caught during the two periods.

At Station 6, the population estimates for small Arctic cisco remained relatively constant between Periods 2 and 3, and there was reasonable agreement between the two census techniques (Table 4). No large Arctic cisco were observed by divers or caught in seine hauls at this location during Periods 2 and 3. This was in marked contrast to the situation at this station during Period 1, when Envirosphere (1986), using both gill nets and diver observations, reported approximately 90 large (>240-mm) and a school of about 100 small (<80-mm) Arctic cisco. It thus appeared that the number of large Arctic cisco decreased between Periods 1 and 2. The physical measurements taken at this station suggested that the entire water

Table 4. Population estimates for fish species at Station 6 based on diver transects during Periods 2 and 3 and seine hauls during Period 2.

Species	Mean density (no./100 m³)	Estimated volume of over-wintering area (100 m³)	Estimated population no.
Diver transects, Period 2			
ARCS (sm)	1.08	180	194
FHSC	1.79	180	322
Diver transects, Period 3			
ARCS (sm)	1.56	130	203
Seine haul, Period 2			
ARCS (sm)	1.91	180	344
FHSC	0.81	180	146

Table 5. Population estimates for fish species at Station 7 based on diver transects during Periods 2 and 3 and seine hauls during Period 3.

Species	Mean density (no./100 m³)	Estimated volume of over-wintering area (100 m³)	Estimated population no.
Diver transects, Period 2			
ARCS (lg)	9.14	286	2,614
BDWF	0.49	286	140
GRAY	1.48	286	423
BURB	0.49	286	140
Diver transects, Period 3			
ARCS (lg)	12.84	273	3,505
ARCS (sm)	0.39	273	106
BDWF	0.42	273	115
GRAY	7.59	273	2,072
RDWF	3.35	273	915
BURB	0.07	273	19
Seine haul, Period 3			
ARCS (lg)	3.91	273	1,067
FHSC	1.76	273	480
LSCS	0.25	273	68
BDWF	1.26	273	344
GRAY	5.29	273	1,444
RDWF	1.01	273	276
BURB	0.63	273	172

column was composed of cold, marine water (28 ppt, −2.0°C) by Period 2. This incursion of cold saline water may have forced the larger Arctic cisco farther upstream to less saline habitats. It was interesting to note that small Arctic cisco were present during both late season periods and thus apparently were able to tolerate higher salinity and lower temperature throughout the winter period.

Population estimates for the various fish species observed or caught at Station 7 generally increased between Periods 2 and 3. This was especially striking for grayling and round whitefish, which increased from 400 to 2,000 and from 0 to 900, respectively (Table 5). Undoubtedly some of the increases can be attributed to nonrandom distribution within the overwintering pool, but some may have resulted from movement of fish into the area as winter progressed. For example, large Arctic cisco and grayling may have moved upstream from the lower delta in front of the marine water wedge described previously. By Period 3 the large number of fish occupying this station appeared to have depleted the dissolved oxygen to levels sufficient to produce mortality. Numerous dead round whitefish and Arctic cisco were observed by divers.

These population estimates, in relation to the amount of habitat, provided an objective comparison between the Sagavanirktok and Colville River deltas in terms of their overwintering potential. The average estimated population of Arctic cisco, giving equal weight to both esti-

mation techniques (seine and diver observation), is 1,339. This population is confined within the Sagavanirktok Delta in approximately 1.3 km of river channel (based upon channel descriptions in Envirosphere 1986). Surveys in this and other areas of the Sagavanirktok Delta by both LGL (this study) and Envirosphere (1986) indicate that overwintering areas are limited, with the western channel providing greater winter habitat potential by virtue of its greater depth.

Observed Mortality

During the third sample period at Station 7, oxygen levels ranged from 0.3 to 2.7 mg/liter. These levels were considerably lower than the mean incipient oxygen response threshold for freshwater species (3.98 mg/liter) or for anadromous, nonsalmonid species (3.38 mg/liter) (Davis 1975; Reiser and Bjornn 1979). Thus, it was suspected that fish at this location were undergoing low-oxygen related stress and mortality. Diver observations at this station on 26 April documented a number of dead fish both on the bottom and at the underside of the ice or frozen into the ice. The fish species found dead were primarily round whitefish (23) with lower numbers of Arctic cisco (one), broad whitefish (one), least cisco (one), and burbot (three).

A sample of dead fish was collected and examined in the laboratory. The initial appearance of the fish indicated that they had undergone severe low-oxygen stress; the opercula were flared and the mouth was gaping. Subsequent laboratory analysis and dissection of these fish found no irregularities such as extreme parasite load or poor condition factor as an alternate hypothesis for mortality. Similar to the live fish taken for stomach analysis, the dead fish had no food in their stomachs except for a small round whitefish (68 mm) that had ingested a larval chironomid.

The low oxygen levels in this pool were probably related to two factors: isolation of the water mass and overcrowding. This station was apparently contiguous with Station 6 earlier in the season since a large concentration of fish migrated upstream from Station 6 to Station 7, probably in response to the intrusion of more saline waters. Later in the season as ice thickness increased, Station 7 became isolated from both Stations 6 (downstream) and 1 (upstream). This isolation, in addition to the high densities of fish, no doubt influenced the low oxygen conditions.

Age-Length and Maturity

Otolith-derived ages and sexual maturities were determined for the three most abundant species, Arctic and least cisco and broad whitefish, caught during the study. These results were used for comparisons between the two deltas and with summer season catches from Simpson Lagoon.

Arctic Cisco

Arctic cisco collected from the Sagavanirktok Delta ranged from 1 to 8 years, with the majority being 6-year-olds; conspicuous by their absence were individuals from the 2–4-year age classes (Table 6 and Fig. 6). These results are consistent with the theory that age-0 Arctic cisco originate in the Mackenzie River and take up residence in some Alaskan rivers. In this case, the age-1 and age-6 fish represent the 1985 and 1979 year classes, respectively—the 2 years in which large numbers of Arctic cisco moved into the region (Griffiths and Gallaway 1982; Critchlow 1983; Moulton et al. 1985; Envirosphere 1986; Fawcett and Carpenter 1986; Moulton 1989).

Results from the Colville Delta were not as clear, because only gill nets were used and these are known to select preferentially for larger fish. Arctic cisco ages ranged from ages 5 to 9, with the majority in the 6- and 7-year age classes (Table 7), which would suggest large migrations into the Colville Delta in both 1978 and 1979. Although none were caught during our winter sampling, a major immigration of age-0 Arctic cisco into the Colville Delta occurred in the summer of 1985 (Fawcett and Carpenter 1986; Moulton 1989).

The age–length relationship for Arctic cisco based upon 1985–1986 winter samples appeared to be similar between the samples obtained from the Colville and Sagavanirktok River deltas. Length-at-age estimated from these samples appeared lower than that of the 1978–1979 samples from Simpson Lagoon. This is not unreasonable since the Simpson Lagoon samples were taken in midsummer where fish of the same "age" would have benefitted from the addition of part of another growing season.

Least Cisco

The age–length relationship and age-specific maturity of least cisco collected in the Colville Delta are given in Table 8 and are compared with the results from the Simpson Lagoon study in Figure 7. Least cisco in the Colville Delta ranged in age from 5 to 13; younger fish were not represented because the gill nets were biased for large individuals (Table 8). The growth rate of these fish was generally similar to that reported for Simpson Lagoon (Craig and Haldorson 1981; Fig. 7). The slightly higher growth rates of Simpson Lagoon fish may be attributed to the mid-summer collection of those specimens.

Broad Whitefish

Broad whitefish were larger for a given age and tended to live longer than either Arctic or least cisco (Table 9 and Fig. 8). The ages for this species ranged from 2 to 21 years, with maturity being reached between ages 8 and 11. These results were similar to those reported for broad whitefish in Simpson Lagoon (Craig and Haldorson 1981).

Table 6. Age, length, and maturity of Arctic cisco collected in the Sagavanirktok Delta during winter 1985–1986. Data from all sample periods are combined.

					Maturity				
					Male		Female		Unid.:
Age	No.	Mean	Range	SD	No.	% Mat.	No.	% Mat.	no.
1	9	59.9	52–69	5.2	0	—	0	—	9
2	0	—	—	—	0	—	0	—	0
3	0	—	—	—	0	—	0	—	0
4	0	—	—	—	0	—	0	—	0
5	2	259.0	237–281	31.1	0	—	2	0	0
6	19	283.9	258–327	17.8	1	0	18	0	0
7	3	279.0	239–320	40.5	0	—	3	0	0
8	1	338.0	—	—	0	—	1	0	0
Total	34				1		24		9

Condition: Length/Weight Relationships

Fish restricted to river or delta habitats over the long winter period are confronted with surviving in an extremely harsh environment. The limitations placed on the fish include reduced space, food availability, and in some areas reduced oxygen levels. In addition, freezing temperatures and marine water intrusions could further tax the metabolic and physiological requirements of the fish. It seems reasonable to expect the general condition of overwintering fish populations to deteriorate as winter progresses and that one overwintering area may be better than another.

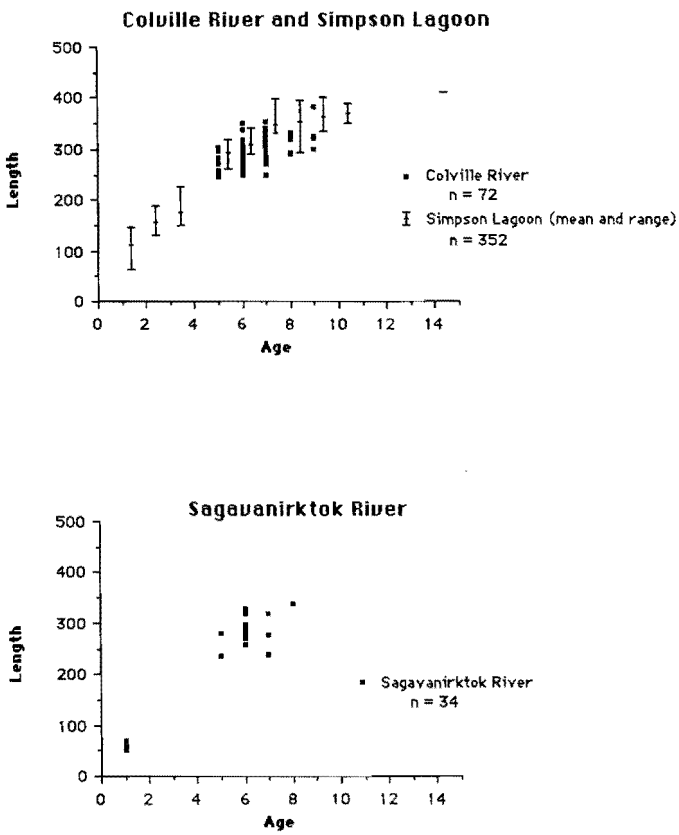

Figure 6. Age–length relationship for Arctic cisco collected in the Colville and Sagavanirktok Deltas during the winter of 1985–1986. Results from Simpson Lagoon in summer (Craig and Haldorson 1981) are shown for comparison. To prevent overlap the Simpson Lagoon data have been shifted to the right.

A scheme of orthogonal contrasts was designed to allow comparisons of fish catch in early vs. late winter and Sagavanirktok vs. Colville Deltas. A complete listing of contrasts and results of F-tests for both equality of slopes and of adjusted mean weights is given in Table 10. For each data set, lengths and weights were subjected to natural log transformations and then regressed. The regressions were compared using analysis of covariance (Hicks 1973; Neter and Wasserman 1974). If slopes were similar, the difference between the adjusted mean weights (weight at the mean length of the pooled sample) was used to evaluate condition. The results of the analysis of covariance (Table 10) indicate significant differences in mean weight at the adjusted mean length for large Arctic cisco, least cisco, and broad whitefish when comparing samples from Period 1 to Periods 2 and 3 combined. For broad whitefish the difference in adjusted mean weight indicates that condition decreased, that is, fish of a given length lost weight during the time between Period 1 and Period 2 (Table 10 and Fig. 9). This does not seem unusual because of the a priori expectation for a lower mean weight at the end of a winter season, especially when feeding appears to be minimal (see below). Arctic and least cisco exhibit the opposite trend with mean weights during Periods 2 and 3 being higher than those during Period 1.

Comparison 3 (Table 10) for large Arctic cisco in the Colville Delta indicates that during Period 1 this species had a significantly higher mean weight at the adjusted mean length than those in the Sagavanirktok Delta. This suggests that Colville Delta fish, as a group, began the overwintering season in better condition than their counterparts in the Sagavanirktok Delta. During Periods 2 and 3, there was no difference between these two groups (comparisons 4 and 5). These early winter differences may be

Table 7. Age, length, and maturity of Arctic cisco collected in the Colville Delta during winter 1985–1986. Data from all sample periods are combined.

					Maturity				
					Male		Female		Unid.:
Age	No.	Mean	Range	SD	No.	% Mat.	No.	% Mat.	no.
5	12	271.6	244–304	20.6	0	—	11	0	1
6	25	284.0	247–349	27.5	0	—	20	5	5
7	23	302.0	249–352	27.9	0	—	20	15	3
8	8	307.9	289–332	18.0	1	100	7	14	0
9	4	332.5	300–383	35.5	0	—	4	0	0
Total	72				1		62		9

due at least in part to disproportionate summer feeding opportunities.

Small Arctic cisco, which were found only in the Sagavanirktok River delta, showed no significant differences in slope or adjusted mean weight between any of the sampling periods. This may suggest good survivorship during winter; however, small sample sizes preclude definitive analysis (Table 10).

WINTER FEEDING AND FOOD AVAILABILITY

Arctic anadromous species vacate coastal waters between mid-July and September, and return to overwintering areas in rivers, delta channels, and lakes (Craig 1989). These fish then spend the next 8 to 9 months in confined sites. The question as to whether these fish continue to feed throughout the long winter period or maintain themselves on fat reserves accumulated in the preceding summer has not been addressed fully in previous winter studies. To address this data gap, stomach samples from the key anadromous species were collected in the Colville and Sagavanirktok Deltas. In addition, food availability was determined from drop-net and Ponar grab collections for epibenthic and infaunal invertebrates, respectively. These data were used to examine the incidence and nature of feeding for fish overwintering in the Colville and Sagavanirktok Deltas.

Stomach Contents

In the Sagavanirktok Delta, virtually all anadromous and freshwater fish stomachs examined were empty, indicating that fish in this region did little if any feeding throughout the winter period. Nevertheless, all of the 11 fourhorn sculpin stomachs examined from the lower reaches of the delta and nearshore coastal waters contained prey, predominantly mysids.

Stomach samples taken from Arctic and least cisco in the Colville Delta contained prey, in each of the three sampling periods, with the exception of least cisco in Period 3. Overall, the percentage of specimens containing food was somewhat over 30 percent; however, the volume of prey items was small. Craig and Haldorson (1981) also reported winter feeding by least and Arctic cisco during the winter of 1978–1979 but that the number of specimens containing food was much higher.

In almost all collections, the unidentified portion of the

Table 8. Age, length, and maturity of least cisco collected in the Colville Delta during winter 1985–1986. Data from all sample periods are combined.

					Maturity				
					Male		Female		Unid.:
Age	No.	Mean	Range	SD	No.	% Mat.	No.	% Mat.	no.
5	4	221.3	193–244	21.3	0	—	3	0	1
6	11	237.5	201–295	27.8	2	0	7	43	2
7	22	255.3	198–296	24.1	6	33	16	69	0
8	3	256.7	249–271	12.4	2	0	1	0	0
9	2	286.0	275–297	15.6	0	—	2	100	0
10	5	294.4	278–318	16.3	0	—	4	75	1
11	2	302.0	278–326	33.9	0	—	2	100	0
12	4	301.3	289–317	12.0	1	0	3	100	0
13	1	279.0	—	—	0	—	1	100	0
Total	54				11		39		4

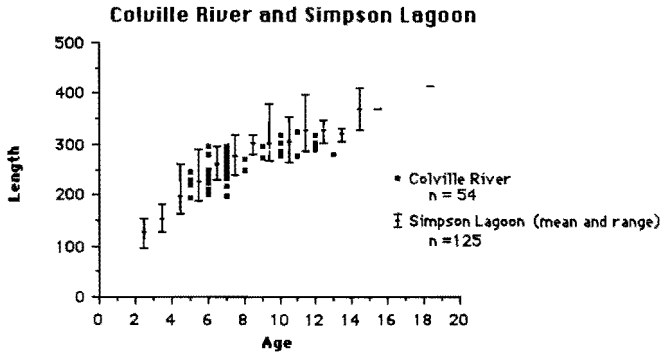

Figure 7. Age–length relationship for least cisco collected in the Colville Delta during the winter of 1985–1986. Results from Simpson Lagoon in summer (Craig and Haldorson 1981) are shown for comparison. To prevent overlap the Simpson Lagoon data have been shifted to the right.

stomach contents represented a significant part of the total: 26–35 percent for fourhorn sculpin, 36–68 percent for Arctic cisco, and 0.2–28 percent for least cisco. Amphipods were the dominant prey item of the Arctic cisco that had prey in their stomachs during each of the three periods, representing from 19 to 62 percent of the total. The only other prey items that contributed to the diet were isopods (4.2%) in Period 1, polychaetes (1.6%) and mysids (0.7%) in Period 2, and polychaetes (13.6%) during Period 3. Craig and Haldorson (1981) also found that Arctic cisco collected in late winter in the Colville Delta had been feeding primarily on amphipods (99%) with minor contributions from mysids and polychaetes.

Least cisco from the Colville River delta that had prey in their stomachs fed almost exclusively on amphipods during Periods 1 and 2; all 14 stomachs from Period 3 collections were empty. Least cisco collected in the Colville River delta during April–May 1978 had similar diets in that they had fed entirely on amphipods (Craig and Haldorson 1981).

Thus, it appeared that some Arctic and least cisco in the Colville River delta fed during the winter, in at least the two widely separated years in which they have been sampled. In contrast, Sagavanirktok Delta Arctic cisco did not appear to feed at any time throughout the winter even though prey was available.

Prey Availability

Generally, estimates of the amounts of prey accessible to fish in the various aquatic and marine habitats in the Alaskan Arctic have varied widely. Craig (1989) estimates that prey densities have ranged from a low of about 0.1 g/m^2 in "Mountain Streams," to medium levels of 0.24 g/m^2 in "Coastal Plain and Tundra Streams," to a high of approximately 1.2 g/m^2 in "Coastal Waters."

The amounts of prey estimated to have been available to fishes in each of the two delta habitats by station grouping and sampling period are shown in Figure 10. In the

Table 9. Age, length, and maturity of broad whitefish collected in the Sagavanirktok Delta during winter 1985–1986. Data from all sample periods are combined.

					Maturity				
					Male		Female		Unid.:
Age	No.	Mean	Range	SD	No.	% Mat.	No.	% Mat.	no.
2	7	114.1	111–122	4.9	0	—	0	—	7
3	0	—	—	—	0	—	0	—	0
4	3	251.1	239–261	11.2	0	—	2	0	1
5	4	300.0	272–320	20.3	0	—	4	0	0
6	10	318.8	277–361	26.3	0	—	6	0	4
7	27	335.6	308–362	15.2	2	0	20	0	5
8	5	354.0	320–387	30.3	0	—	5	20	0
9	2	361.5	321–402	57.3	1	100	1	0	0
10	1	324.0	—	—	0	—	1	100	0
11	1	423.0	—	—	1	100	0	—	0
12	2	438.5	431–446	10.6	1	100	1	0	0
13	2	451.0	443–459	11.3	1	100	1	100	0
14	2	415.5	410–421	7.8	0	—	2	50	0
15	0	—	—	—	0	—	0	—	0
16	1	438.0	—	—	0	—	1	0	0
17	0	—	—	—	0	—	0	—	0
18	0	—	—	—	0	—	0	—	0
19	1	410.0	—	—	0	—	1	100	0
20	0	—	—	—	0	—	0	—	0
21	1	480.0	—	—	1	100	0	—	0
Total	69				7		45		17

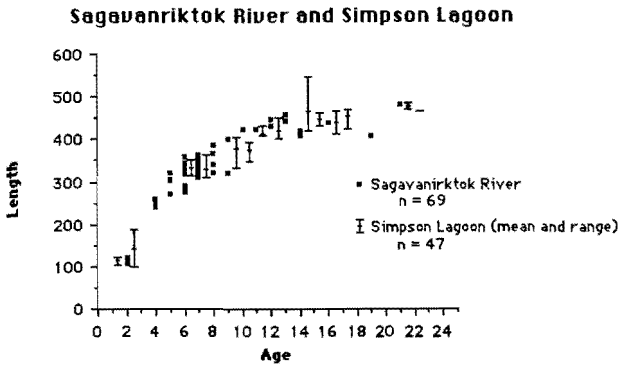

Figure 8. Age–length relationship for broad whitefish collected in the Sagavanirktok Delta during the winter of 1985–1986. Results from Simpson Lagoon in summer (Craig and Haldorson 1981) are shown for comparison. To prevent overlap the Simpson Lagoon data have been shifted to the right.

Sagavanirktok Delta, Station 1 was treated separately since its waters remained fresh during the winter, Stations 2 and 3 were grouped as marine sites, and Stations 6 and 7 were grouped as lower delta sites. In the Colville Delta, a single station was sampled during each period.

As expected, freshwater organisms (plecopteran and ephemeropteran nymphs, and tipulid and chironomid larvae) comprised the available prey at Station 1. The total amount present varied with sampling period (range 0.1–0.31 g/m^2) and the dominant group changed from tipulids in Periods 1 and 3 to ephemeropterans in Period 2 (Fig. 10). Low levels of prey found at this station were similar to those reported for "Mountain Streams" along the North Slope by Craig (1989).

Stations 6 and 7 in the Sagavanirktok River delta were sampled only during Periods 2 and 3. During both periods isopods were the most abundant prey organism reported (17 and 80 g/m^2, respectively). Only two other groups

Table 10. Orthogonal contrast scheme for large and small Arctic cisco, least cisco, and broad whitefish from scientific catches in the Sagavanirktok and Colville Rivers during winter 1985–1986. Sample sizes, slopes, and adjusted means of the natural log of weight (g) are given.

No.	Description	*N*	Slope	*F*	Adj. mean wt.	*F*
	Large Arctic cisco					
1	Period 1, Sag. & Colville vs.	187	3.322	1.012 ns	5.58	17.698*
	Periods 2 & 3, Sag. & Colville	104	3.137		5.60	
2	Period 2, Sag. & Colville vs.	56	3.115	0.006 ns	5.66	0.553 ns
	Period 3, Sag. & Colville	48	3.126		5.67	
3	Period 1, Colville vs.	142	3.364	0.075 ns	5.57	74.670*
	Period 1, Sag.	45	3.321		5.47	
4	Period 2, Colville vs.	13	3.571	2.752 ns	5.62	0.169 ns
	Period 2, Sag.	43	3.007		5.61	
5	Period 3, Colville vs.	8	2.850	1.552 ns	5.73	0.306 ns
	Period 3, Sag.	40	3.227		5.73	
	Small Arctic cisco (Sag. only)					
1	Period 1 vs.	10	2.542	0.195 ns	0.64	0.296 ns
	Periods 2 & 3	40	2.951		0.61	
2	Period 2 vs.	26	2.604	1.543 ns	0.48	0.669 ns
	Period 3	14	3.161		0.52	
3	Period 3, Station 7 vs.	10	2.611	0.926 ns	0.66	2.651 ns
	Period 3, Station 6	4	3.967		0.46	
	Least cisco (Colville only)					
1	Period 1 vs.	62	2.935	1.346 ns	5.18	19.249*
	Periods 2 & 3	37	3.093		5.26	
2	Period 2 vs.	23	3.128	0.903 ns	5.29	2.843 ns
	Period 3	14	2.844		5.23	
	Broad whitefish (Sag. only)					
1	Period 1 vs.	12	3.166	0.155 ns	6.25	27.865*
	Periods 2 & 3	64	3.238		6.13	
2	Period 2 vs.	36	3.238	0.002 ns	6.14	0.235 ns
	Period 3	28	3.237		6.15	

* Significant to <0.05; ns = not significant.

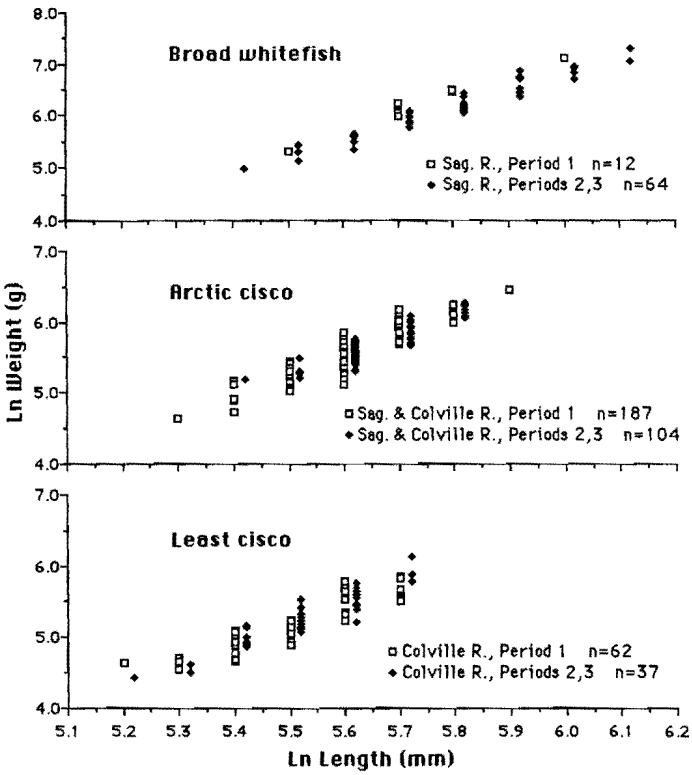

Figure 9. Length/weight relationships for broad whitefish, Arctic cisco, and least cisco. Data were pooled to equally spaced transformed length intervals.

contributed to the available prey at these stations: mysids (0.15 g/m^2) in Period 2 and amphipods (0.72 g/m^2) in Period 3 (Fig. 10).

Isopods are not commonly eaten by Arctic and least cisco or broad whitefish during the open-water season (Moulton et al. 1985). If this group is not included in the accessible food category, then at Station 7 the level of available food becomes 1.6 and 4.1 g/m^2 during Periods 2 and 3, respectively; at Station 6 the levels are much lower, 0.2 and 0.7 g/m^2 for Periods 2 and 3, respectively (Table 11).

The nearshore waters, represented by Stations 2 and 3, contained comparable or slightly higher levels of prey organisms (1.7–2.5 g/m^2; isopods, bivalves, and polychaetes excluded) throughout the winter (Table 11) than the open-water season average reported by Craig (1989). Isopods, mysids, and amphipods were the dominant epibenthic organisms, while bivalves and polychaetes dominated the infaunal community (Fig. 10). Even though prey were abundant at nearshore stations, few marine fish species and no anadromous species were collected at these locations during winter.

Prey levels at the Colville Delta station showed no consistent pattern over the winter sampling period (Fig. 10). Total levels fluctuated from greater than 15 g/m^2 in Period 1 to 0.01 g/m^2 during Period 2, and the dominant group varied from amphipods to gastropods in Periods 1 and 3, respectively (Fig. 10). Except for Period 1, prey levels in the Colville Delta were lower than those in the Sagavanirktok Delta (Table 11). Despite this, some Arctic and least cisco fed throughout the winter in the Colville River, but the amount of biomass consumed was small and not dependent upon prey availability.

DISCUSSION

The results of the overwintering study in the Sagavanirktok River delta suggest that the size of the overwintering habitat is small (estimated 1.3 km of deep-pool habitat) and mostly restricted to the west channel. An estimated 1,000–3,000 Arctic cisco overwintered in this habitat, predominantly large fish of the 1979 year class. Despite the occurrence of thousands of young-of-the-year Arctic cisco in adjacent coastal waters late in the 1985 open-water season (Envirosphere 1986), only a few hundred were estimated to have overwintered in the west delta and nearshore sites. The implication is that the vast majority of age-0 fish had passed from east to west through the area. Supporting this contention is (1) the observation from Envirosphere (1986) that there was apparently no significant blockage resulting from the area causeways, and (2) the observed recruitment of this age group into the Colville River delta in late summer/early fall 1985 (Moulton et al. 1986).

In comparison, the Colville River delta is estimated to contain on the order of 220 km of main-channel habitat. Moulton et al. (1986) estimated the number of Arctic cisco greater than 250 mm fork length, alone, was likely on the order of one to two million fish. It should also be noted that the Colville River channels are characteristically deeper than the Sagavanirktok River delta channels. As winter progresses, pool habitats within the Sagavanirktok River delta become isolated by ice freezing to the bottom, thereby restricting fish movement and access to other areas of the delta. In the Collville River delta, fish are able to move about over a wider area of the delta because of the greater depth of the channels.

Arctic cisco in the Sagavanirktok River delta mainly resided in brackish waters (on the order of 5 ppt) and were not characteristic in either marine or freshwater pools. Some movement in apparent response to increased salinity was observed prior to the isolation of the study pools. A similar movement pattern may account for the marked decline in cisco catches in the Colville River in late as compared to early winter.

Anadromous and freshwater fish collected from the Sagavanirktok River delta did not exhibit any feeding over the winter period. In the Colville Delta, in excess of 30 percent of the specimens collected had fed to at least some degree. Amphipods were the predominant prey ingested. No significant increases in length were observed over the winter for any species.

Results of comparisons of cisco condition over the win-

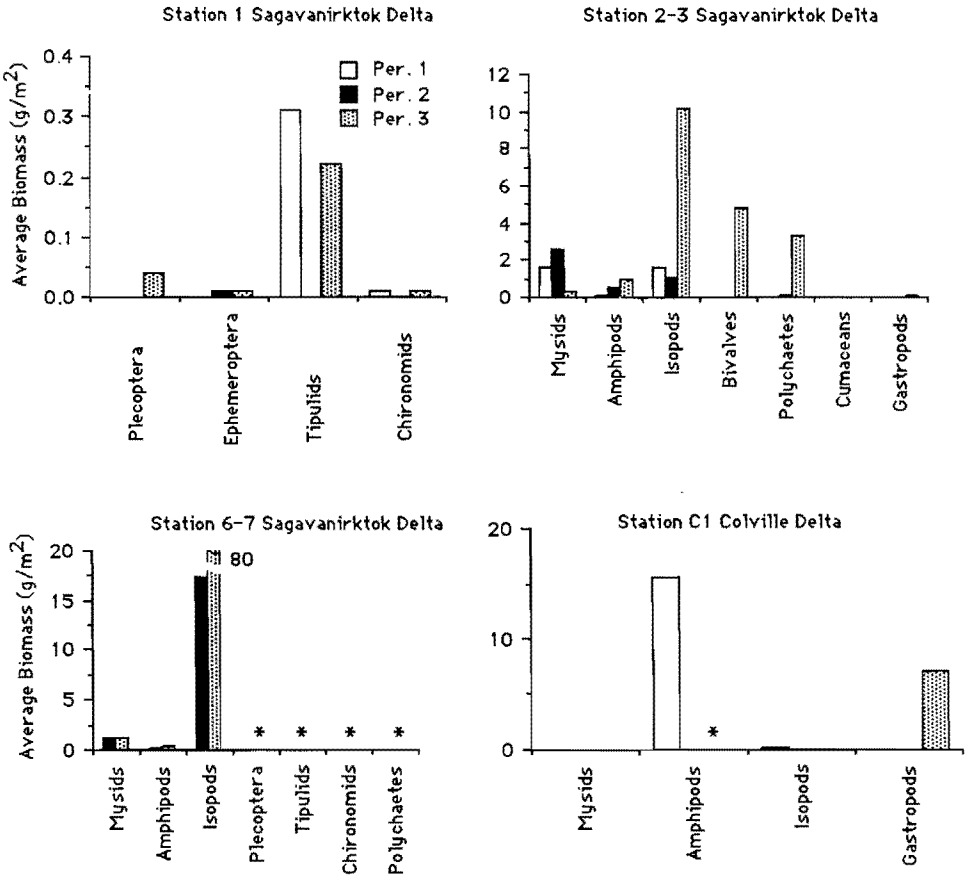

Figure 10. Average biomass (g/m² wet weight) of epibenthic and infaunal invertebrates at stations in the Sagavanirktok and Colville Deltas in winter 1985–1986. * Indicates mean <0.5 g/m².

ter and between the two sites were surprising. The general trend for both areas was a significant increase in condition in late winter as compared to early winter. This phenomenon is counter-intuitive but explicable based upon the length/weight plots. For both Arctic and least cisco (Fig. 9) the increase in mean weight is clearly attributable to the absence of lighter individuals across the length range in late season samples, as compared to the early season. In all likelihood, the lighter fish at a given length had not attained sufficient energy reserves during the preceding summer season to survive the winter.

The only significant difference in condition of fish between the two sites was in early winter when Arctic cisco from the Colville Delta exhibited significantly better condition than Arctic cisco from the Sagavanirktok Delta. Given that some Colville fish fed over the winter, whereas fish from the Sagavanirktok did not, one would have expected such differences to occur late in the season. Further, early winter differences would not be expected if food is typically not limiting in coastal waters, as generally believed (e.g., Craig and Haldorson 1981; Moulton et al. 1985).

This early season difference suggests that Arctic cisco associated with the Sagavanirktok Delta did not fare as well as their counterparts from the Colville Delta in the summer of 1985. The reasons for this phenomenon are unknown but may be related to poorer feeding opportunities or unfavorable physical conditions during the summer for the cisco overwintering in the Sagavanirktok Delta.

Arctic anadromous fish are believed to vacate marine waters to overwinter in less saline habitats in order to avoid actual freezing of their tissues by the supercooled waters found in marine habitats during winter (Craig 1984,

Table 11. Total average biomass (g/m²) of fish prey available* at stations within the study area during the winter of 1985–1986.

Station	Period 1	Period 2	Period 3
Sagavanirktok Delta			
Station 1	0.3	0.01	0.2
Stations 2 & 3	1.7	2.5	2.0
Station 6	NS†	0.2	0.7
Station 7	NS	1.6	4.1
Colville Delta			
Station C1	15.0	0.01	0.01

* Isopods, bivalves, polychaetes, and gastropods excluded.
† NS = not sampled.

1989). Thus, the primary adaptation to the cold, winter environment appears largely behavioral in nature. Other Arctic and Antarctic forms exhibit different adaptations. In the Arctic, deep-water marine fishes can remain supercooled, below the freezing point of blood, indefinitely, while shallow-water species (e.g., fourhorn sculpin) raise the osmotic pressure of their blood (Dunbar 1968). Antarctic invertebrates are able to maintain hypersomatic tension within their cell walls (Clarke 1980) and several species of fish sequester glycoproteins in body fluids, thus preventing freezing (DeVries and Lin 1977). Whether some of these adaptations are also incorporated by arctic anadromous fish is unknown.

Another behavioral adaptation to reduce energy expenditure during winter might be to maintain a position in the salinity gradient such that energy required for osmoregulation is reduced. For freshwater fish, this is likely on the order of 8 to 9 ppt (Doudoroff 1967). The distributional and movement patterns of the ciscoes are suggestive of such a response.

In addition to mortality resulting from inadequate energy reserves, arctic anadromous fish also must cope with the potential overcrowding of the overwintering habitat. Such an event occurred during the course of this study. A relatively large number of fish moved into a pool characterized by near-optimum salinities for osmoregulation (~5 ppt). By February–March, this pool was isolated from up- and downstream areas by ice. Between this time and late April–early May, dissolved oxygen levels were depleted, and a fish kill resulted. It is likely that the oxygen depletion resulted from overcrowding.

Of interest, the overcrowding was not attributable to the abundance of small (age-0 or -1) Arctic cisco, which numbered only a few hundred as opposed to one to several thousand large Arctic cisco and other species. On a biomass basis, the contrast was even more pronounced. The small Arctic cisco were not observed to be abundant in any habitat, nor did the condition of the samples suggest any loss of condition over the winter.

Naturally occurring fish kills have not been reported frequently, probably due to the low number of winter studies conducted. At least one natural kill has been reported in the Upper Dietrich River (Chihuly et al. 1979) and another suspected kill was reported in the mid-reaches of the Sagavanirktok River (Bendock and Burr 1984). Although the individual fish experiencing this situation were lost to the population, arctic anadromous fish as a whole have reduced their chances of extinction by spreading their members over more than one overwintering site (Craig 1989).

Results from this study as well as Craig and Haldorson (1981), Bond (1982), and Envirosphere (1986) show that both Arctic and least cisco overwinter in nearshore areas including harbors and deltas, and that both small and large Arctic cisco utilize the same habitats. These studies, although intense, were restricted geographically. More extensive studies in the Mackenzie, Canning, and Kongakut Deltas or Demarcation Bay, for example, may reveal more overwintering areas.

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Localized Movement Patterns of Least Cisco (*Coregonus sardinella*) and Arctic Cisco (*C. autumnalis*) in the Vicinity of a Solid-Fill Causeway

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Abstract. This paper assesses the short-term movements and distribution of two species of ciscoes (*Coregonus autumnalis* and *C. sardinella*) in relation to a solid-fill causeway (West Dock) based upon results of studies conducted in Prudhoe Bay from 1981 through 1985. When winds blow from the east, West Dock modifies nearshore hydrographic and circulation regimes to such an extent that the eastward dispersals of ciscoes are delayed or blocked. Under the reversed situation (westerly winds confronting westward-dispersing ciscoes), the effects of West Dock are less clear-cut. Local conditions largely determine whether one of these man-constructed intrusions may seriously affect a delicate, fragile environment, or may be insignificant quirks to populations that have survived millennia of such adversities.

INTRODUCTION

The commercial development of petroleum reserves in Prudhoe Bay, Alaska, has prompted scientific studies aimed at assessing the impact of industrial activity upon the local and regional marine environments. Particular concern has centered on the construction of solid-fill causeways along the Arctic coast and the effects these structures may have upon the alongshore migration and habitat utilization of arctic anadromous fish. In response to these concerns, and as part of the regulatory process, industry has funded fish monitoring surveys in the Prudhoe Bay region each summer since 1981. Collectively, these studies represent one of the most detailed and comprehensive sets of fishery investigations in the North American Arctic.

This paper assesses the short-term movements and distributional patterns of least cisco (*Coregonus sardinella*) and Arctic cisco (*C. autumnalis*) in relation to a solid-fill causeway based upon results of the 1981–1984 Prudhoe Bay fishery studies. These species were targeted because both are abundant in coastal waters and support subsistence and commercial fisheries. Emphasis is placed on identifying the roles of water temperature, salinity, current, and coastal topography in modifying the alongshore migration of these two anadromous fish species.

Data for the Prudhoe Bay studies were collected and originally reported by Griffiths and Gallaway (1982), Critchlow (1983), Griffiths et al. (1983), Woodward-Clyde Consultants (1983), Biosonics, Inc. (1984), and Moulton et al. (1986). Data analyses employed the Arctic Anadromous Fish Data Base developed by Baker et al. (1986).

Although we believe this paper presents some new perspectives, observations, and quantitative analyses, many of the concepts regarding movement of fish in Prudhoe Bay have been reported previously. To note each contribution would require an overwhelming series of citations. We therefore cannot express strongly enough the scientific contributions made by Griffiths and Gallaway (1982), Critchlow (1983), Griffiths et al. (1983), Woodward-Clyde Consultants (1983), Biosonics, Inc. (1984), Moulton et al. (1986), and Cannon et al. (1987a).

STUDY AREA

The 1981–1984 studies focused on 120 km of coastline that extends between the Colville and Sagavanirktok (Sag) Rivers (Fig. 1). These two rivers are the largest and second largest drainages on the Alaskan North Slope, respectively. The Sag River is characterized by a 16-km-wide delta that is fronted by a shallow shoal (<1.5 m deep) extending seaward for 3–4 km. Immediately west of the Sag Delta is Prudhoe Bay. It is approximately 7 km across with a maximum depth of 2.5 m. The northern boundary of the bay is formed by a series of shallow shoals (<1 m deep) that extend to the northeast and southwest from centrally located Gull Island (Fig. 2). West Dock causeway, situated at the western edge of Prudhoe Bay, is a solid-fill jetty that extends seaward for 4 km. It is interrupted at the 2.8-km mark by a 15-m-wide breach specifically installed as a fish passageway. Much of the coastline extending westward from the causeway to the Colville River is protected by a 60-km-long chain of offshore barrier islands. The barrier islands enclose a series of shallow lagoons (generally <2 m deep) running from West Dock to Oliktok Point. Seaward of the barrier islands, ocean depths increase to 2–3 m within 50 m from shore. The Colville River, which empties into Harrison Bay, marks the western limit of the study area.

FIELD METHODOLOGY

Fyke nets were the primary sampling gear employed during the 1981–1984 studies. Net locations are depicted

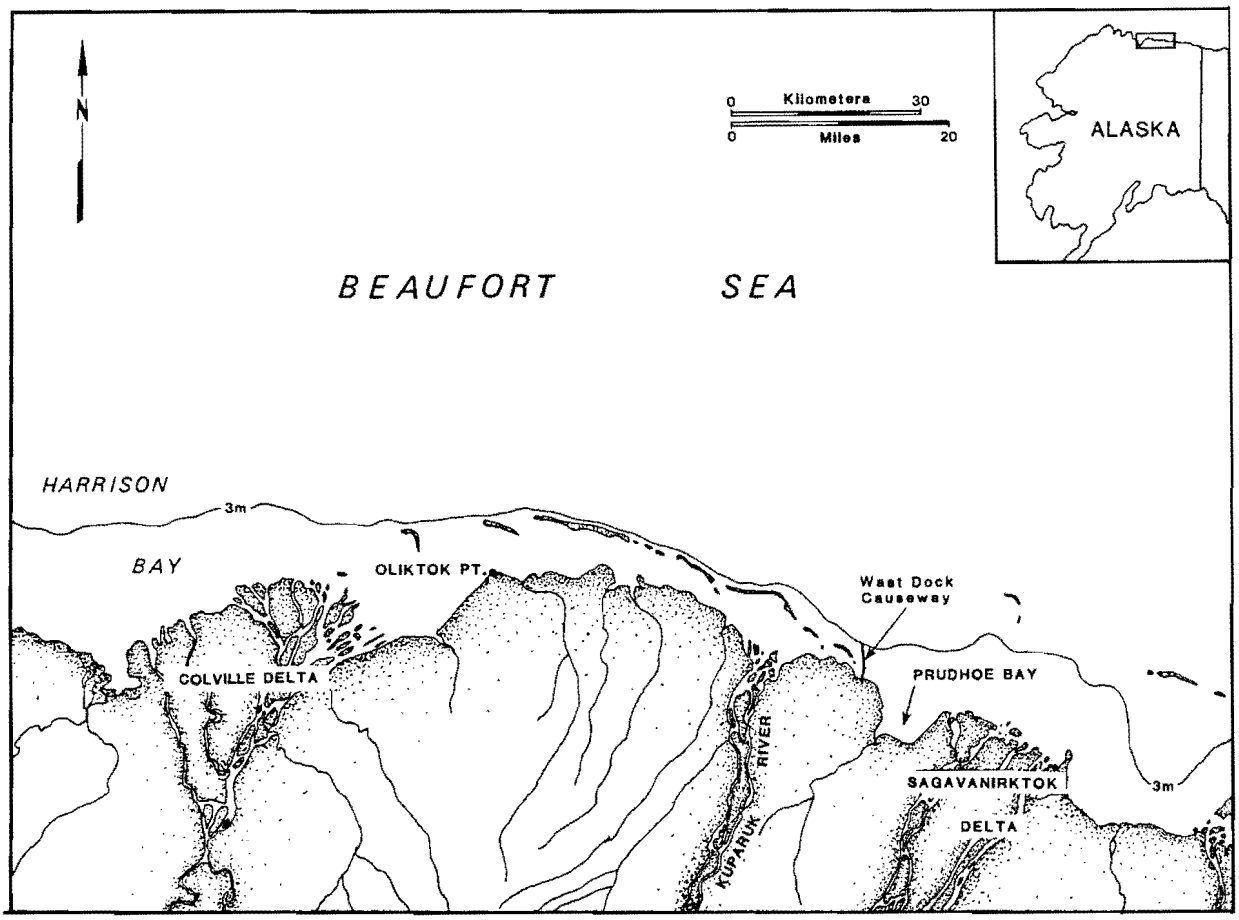

Figure 1. Study area.

by year in Figure 2. Although sampling sites differed among years, sampling regimes were essentially the same. After initial placement, fyke nets were checked daily (weather permitting), and surface water temperature and salinity were measured. Captured specimens were identified to species, enumerated, measured (to a maximum of 200 fish per species per day), and released. Anadromous fish ≥250 mm fork length (FL) were marked with numbered Floy anchor tags (excluding 1983), while specimens measuring 120–249 mm FL were marked using several methods depending upon year (fin clip, 1981, 1982; dye injection, 1982; and freeze-branding, 1982–1984).

Gill nets were also used on a limited basis between 1981 and 1983 and accounted for <1 percent of all anadromous fish collected. The locations, dates, and results of gill-netting efforts will be noted within the text.

Within the text there is frequent reference to "large" (≥250-mm) or "small" (<250-mm) fish. These terms are arbitrary and were originally based upon different field-marking techniques: fish <250 mm were considered too small to be Floy-tagged. This convention has been adhered to in all 4 study years and the same general format will be maintained throughout much of this paper, although specific size cohorts are identified.

Catch is denoted as catch-per-unit-effort (CPUE) and represents either fish/net/day or fish/day. The term "day" specifically refers to a period of 24 hours. All fish lengths reported are fork lengths. Unless otherwise stated, the significance level of all statisitcal tests is $P < 0.05$. All wind data were obtained from meteorological records at Deadhorse Airport, Alaska.

PHYSICAL PROCESSES

Movements of anadromous fish are linked to water temperature, salinity, and current regimes. The following section provides a brief summary of physical processes that are essential for understanding associated responses of least and Arctic cisco.

Seasonal Cycle

The marine and estuarine environments of the Beaufort Sea are covered by ice for almost 9 months of the year, with the open-water season typically lasting from late June through late September/early October. In early June, snowmelt from the Brooks Range causes large quantities of fresh water to be discharged from river outfalls along the coast. The infusion of this relatively warm fresh water facilitates ice breakup and reduces nearshore salinities.

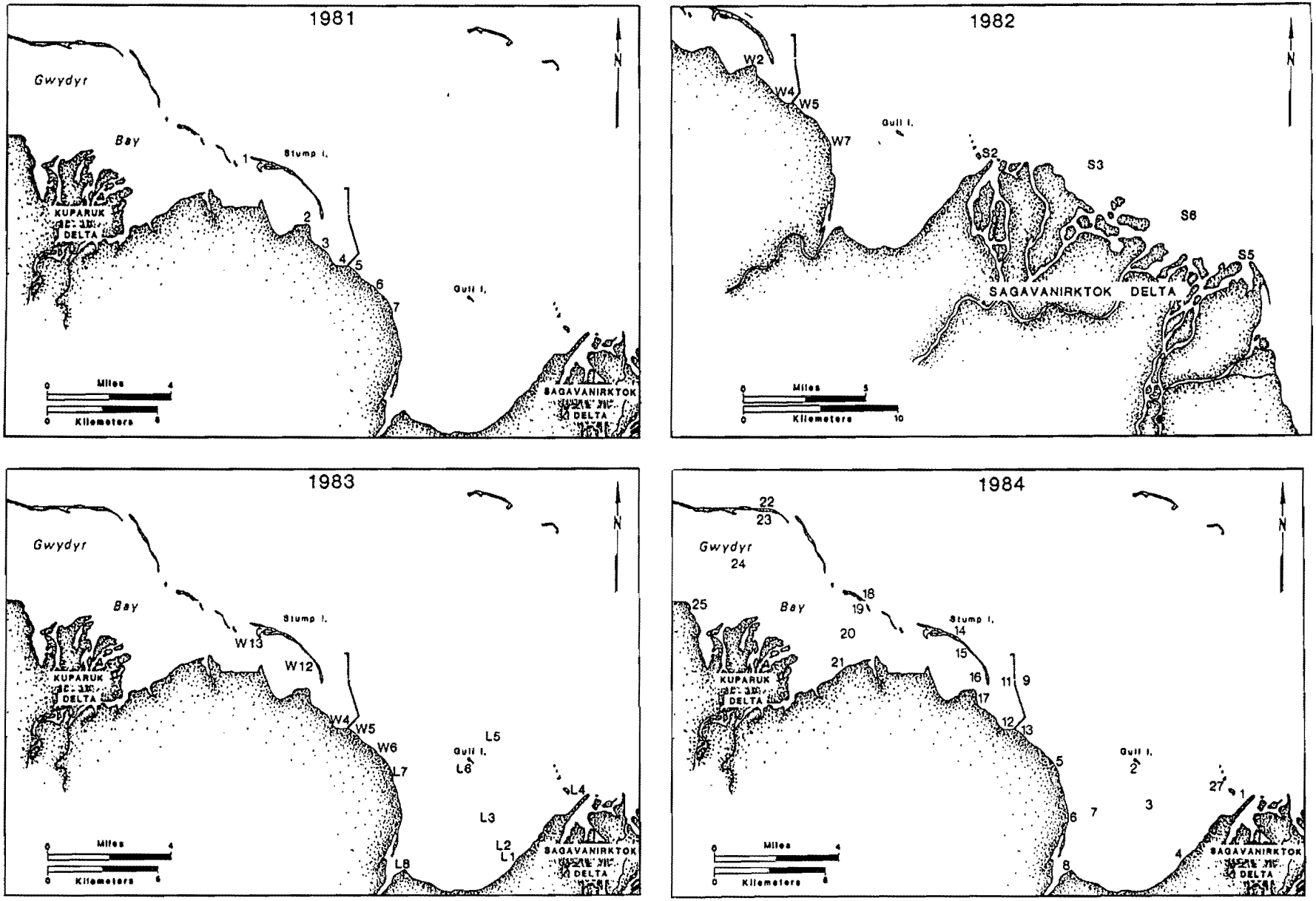

Figure 2. Fyke-net locations for each of 4 study years.

Partial ice cover during the early stages of breakup minimizes wind-driven mixing between nearshore and offshore marine water masses and thus maintains the low salinity environment. As the open-water season progresses, coastal ice cover retreats seaward, wind-driven mixing between nearshore and offshore water increases, and river discharge declines. The result is a rise in nearshore salinity so that by the end of the open-water season levels can exceed 30 parts per thousand (ppt).

The same processes influence nearshore water temperature, but in a slightly different fashion. Solar heating and river discharge are primarily responsible for elevating water temperature during summer. Partial ice cover during breakup not only prevents solar heating, but also acts directly as a cooling agent, thus depressing nearshore water temperatures. As ice dissipates, solar heating and river runoff warm coastal waters, and by July temperatures generally reach their seasonal maxima. Thereafter, as river discharges diminish, cold marine water begins to dominate the nearshore environment. This, in conjunction with reduced daylight (solar heating) and colder air in late summer, causes further cooling of nearshore waters. By late September/early October, water temperatures are near freezing and ice formation in the nearshore areas begins.

Local Hydrographic Patterns

The following brief description of local physical processes is taken primarily from Savoie and Wilson (1986), but includes the cumulative investigative efforts of Barnes et al. (1977), Mungall et al. (1978, 1979), Mungall and Whitaker (1979), Savoie and Wilson (1983), and Weingartner (1983).

Easterly Winds

Nearshore hydrography is primarily wind-driven. Easterly winds cause an offshore transport of surface water that is partially counterbalanced by an onshore flow of subsurface marine water. The effect is a lowering of water levels along the coast and intrusions of cold, marine bottom water. Strong winds cause cold, marine water to enter the lagoon system through the barrier island channels (Fig. 3A). Marine intrusions between West Dock and Stump Island are exacerbated by the causeway itself because the deflection of alongshore flow at its tip intensifies marine upwellings in its lee.

Warm, brackish water discharge from the Sag River is transported westward during easterly winds. Flow is typically interrupted by West Dock causeway, resulting in an accumulation of discharge water on the structure's eastern side. This produces a buoyant plume that is deflected northward by the causeway and then westward around its tip by westerly flowing offshore surface currents. Dissipation of the plume depends upon specific meteorological and oceanographic conditions, but its presence had been recorded up to 10 km west of the causeway. Strong southeasterly winds can drive the plume farther offshore so that its effect on water quality in Prudhoe Bay is diminished. Northeasterly winds can deflect the plume deeper into Prudhoe Bay. During light winds the surface plume may actually round the causeway and flow into Stump Island lagoon.

Westerly Winds

Westerly winds cause a general downwelling along the coast. This forces bottom marine water offshore while warm, brackish water builds up in nearshore areas. Deflection of the Colville River and Kuparuk River plumes causes warm, brackish water to flow eastward through the lagoon complex and out through the barrier island inlets (Fig. 3B). Water reaching the causeway is deflected northward and then eastward around the tip by offshore surface currents. Flow divergence at the tip of West Dock again causes an upwelling in its lee; however, conditions are not as saline as compared to upwellings that occur west of the causeway during easterly winds. This disparity arises because bottom marine water generally moves onshore during easterly winds and offshore during westerly winds. Upwelled water thus tends to be warmer and less saline during periods of westerly winds.

Conditions in Prudhoe Bay can change dramatically when westerly winds are preceded by prolonged periods of easterly winds. Easterly winds cause marine water to move into the barrier island lagoons and to within a 1–2-m depth contour both east and west of the causeway. A shift to westerly winds initially causes the marine water that has accumulated around the causeway to be pushed past West Dock and into Prudhoe Bay. Such conditions can cause dramatic shifts in the hydrography depending upon the intensity of the original (easterly wind) marine water intrusion. Cold marine water that has been purged from the lagoon and causeway area is followed by warm, brackish water flowing eastward from the Colville and Kuparuk Rivers. If westerly winds continue, this warm water plume flows around the causeway and into Prudhoe Bay and reverses the effects of the preceding marine intrusion.

The Sag River plume is deflected eastward during westerly winds and its influence on water quality in Prudhoe Bay is diminished. The river's effect on local hydrography also decreases during the course of the open-water season because of a rapid decline in the rate of discharge. Flow rate, however, is sufficient to maintain relatively warm, brackish conditions directly in front of the delta throughout much of the summer.

REGIONAL MIGRATION PATTERNS

Arctic anadromous fish overwinter in or near major freshwater drainages of Alaska's North Slope. During the

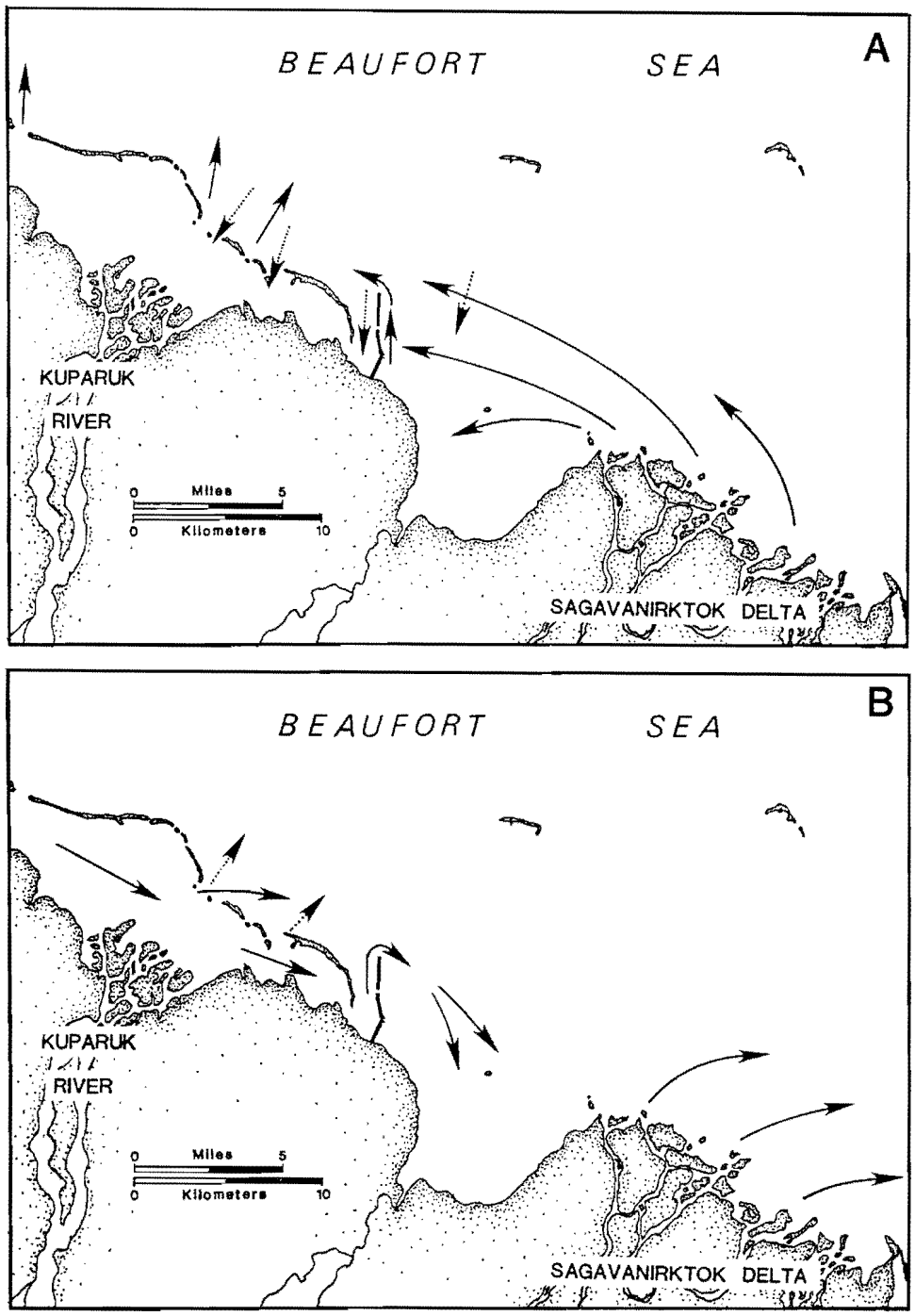

Figure 3. Generalized circulation patterns in the Prudhoe Bay vicinity during (A) easterly and (B) westerly winds. Solid arrows indicate warm, brackish surface currents; dashed arrows indicate cold, marine bottom currents.

brief ice-free summer season, fish disperse into coastal waters to feed (Craig and Haldorson 1981; Moulton et al. 1986). Near the end of summer and prior to freeze-up, fish return to overwintering grounds where they presumably spend the long arctic winter in deepwater holes and channels (Adams 1986; Schmidt et al. 1989).

The Colville River is an important spawning and overwintering area for anadromous least cisco (Alt and Kogl 1973; McElderry and Craig 1981; Fawcett et al. 1986; Schmidt et al. 1989). Conversely, there is little evidence that least cisco use the Sag River for either purpose. Least cisco found in Prudhoe Bay waters thus represent members of the Colville River population that disperse down the coast during the open-water season and return to the Colville prior to freeze-up.

Arctic cisco found in Alaskan waters are believed to be part of a population originating in Canada's Mackenzie River located 500 km west of Prudhoe Bay (Gallaway et

al. 1983). Newly emerged fish are transported into Alaskan waters by alongshore currents and take up residence in coastal zones proximal to major freshwater drainages. Fish are believed to maintain some degree of fidelity to the drainage of residency. They remain in Alaskan waters until the onset of sexual maturity, at which point they return to the Mackenzie River to spawn.

During 1981–1984, most of the large Arctic cisco found near Prudhoe Bay originated from the Colville River (Griffiths and Gallaway 1982; Critchlow 1983; Griffiths et al. 1983; Woodward-Clyde Consultants 1983; Biosonics, Inc. 1984; Moulton et al. 1986; Cannon et al. 1987a). Their appearance and disappearance in daily fyke net catches were consistent with least cisco but not with species that are known to overwinter in the Sag River (e.g., broad whitefish and char). The recovery of tagged individuals in the fall commercial fishery in the Colville River also reflects their return to overwintering grounds in that area.

Unlike least cisco and large Arctic cisco, most small Arctic cisco found near Prudhoe Bay appear to overwinter in the Sag Delta. Small Arctic cisco are taken in fyke-net catches as soon as sampling begins, in many cases long before Colville River fish have arrived on the scene (Griffiths and Gallaway 1982; Critchlow 1983; Griffiths et al. 1983; Woodward-Clyde Consultants 1983; Biosonics, Inc. 1984; Moulton et al. 1986; Cannon et al. 1987a). They are also abundant in the Sag Delta late in the season after Colville River fish have departed. Populations of small Arctic cisco do overwinter in the Colville River (Moulton and Fawcett 1983; Moulton et al. 1986), but during 1981–1984 there were no documented instances of these fish reaching Prudhoe Bay.

It is not completely clear why large and small Arctic cisco are segregated. This trend may have been a phenomenon unique to the 1981–1984 season because of differential recruitment to the Colville and Sag Rivers. For some unknown reason, older year classes may have taken up residency only in the Colville River and years later provided the main source of large Arctic cisco in the study area. Another possibility rests with the differential quality of overwintering habitat. Overwintering areas in the Sag River are far more limited than for the Colville River (Schmidt et al. 1989). Poorer overwintering grounds in the Sag River could mean that few Arctic cisco either survive or remain in the area long enough to become subadults.

LOCAL MOVEMENT (PRUDHOE BAY AREA)

The 1984 study was the largest and most comprehensive of the four surveys and also the most informative for describing fish movement. This study is reviewed first in order to establish a benchmark assessment of fish activity from which to retrospectively gauge the results of previous studies.

1984

The 1984 study was conducted from 22 June to 28 September and surveyed 28 locations—13 sites west of the causeway and 10 to the east (Fig. 2).

Least Cisco

The transient nature of least cisco is evident from seasonal catch patterns. Both large and small fish arrived abruptly in July (Fig. 4). Arrival from the west was indicated by the fact that CPUE began increasing west of the causeway at least 24 hours before fish showed up in Prudhoe Bay. Fish remained in the study area through the middle of the summer, but reductions in CPUE indicated that fish had vacated the area by late August.

Eastward migration. Progressively smaller size classes arrived in the study area on progressively later dates (Fig. 5). This trend probably reflects size-dependent swimming speed. The first group (mode = 320–340 mm) dominated catch west of the causeway prior to 17 July (Fig. 5A). The second size class (mode = 290–300 mm) began arriving on 17 July (Fig. 5B), and another group (mode = 220–240 mm) showed up on 20–21 July (Fig. 5C). The final group of least cisco (modes = 70 and 110 mm) began arriving on 22 July (Fig. 5D). These four size groups will be arbitrarily referred to as Groups 1, 2, 3, and 4.

The 7–8 July influx of Group 1 west of the causeway coincided with westerly winds that had begun to blow on the previous day (Fig. 6B). Eastward flow of the Colville and Kuparuk River plumes caused a sharp increase in lagoon water temperature (Fig. 6A). Surface salinities typically remain low early in the season. The arrival of fish during westerly winds presumably reflects movement in conjunction with the warm-water plume.

Group 1 appeared to move along the mainland shore. During 7–8 July, the period of peak catch activity, mainland Stations 12, 15, 17, 21, and 25 averaged 43.7 fish/net/day (range = 20.5–81.4). Offshore Stations 19, 20, and 23 averaged only 4.0 fish/net/day (range = 1.1–5.0). (No other stations were operational.) The nearshore concentration was not associated with local hydrography over the 2 days because average temperature and salinity differed by only 0.1°C and 0.2 ppt, respectively, between mainland and nonmainland stations. West of the sampling grid, ice was still prevalent in the central portion of the lagoon and along the inside of the barrier islands. This may have contributed to the nearshore distribution.

During the interim period (9–17 July), 90 percent of all fish were caught at mainland Stations 12, 21, and 25 (Fig. 2). This concentration may have been in response to warmer water. Average temperature at these three stations was 7.7°C, compared to 5.2°C for the other lagoon sites. Spearman's Rank Correlation Analysis showed a significant positive association between CPUE and temperature at individual fyke nets during this period (ρ =

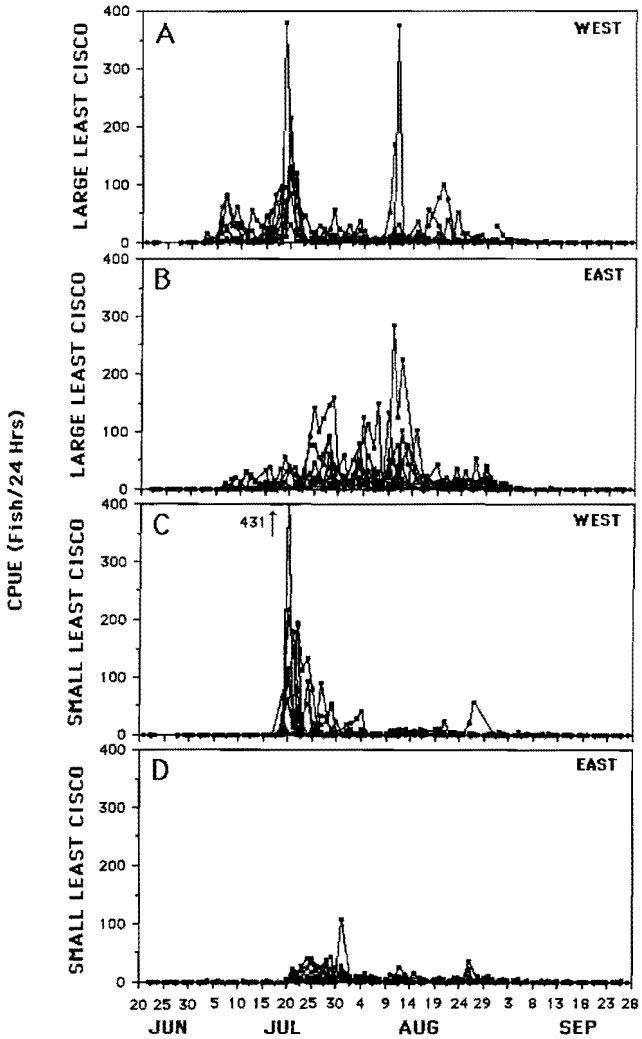

Figure 4. CPUE for large (≥250-mm) and small (<250-mm) least cisco at individual fyke nets located (A, C) west and (B, D) east of the causeway during 22 June–28 September 1984.

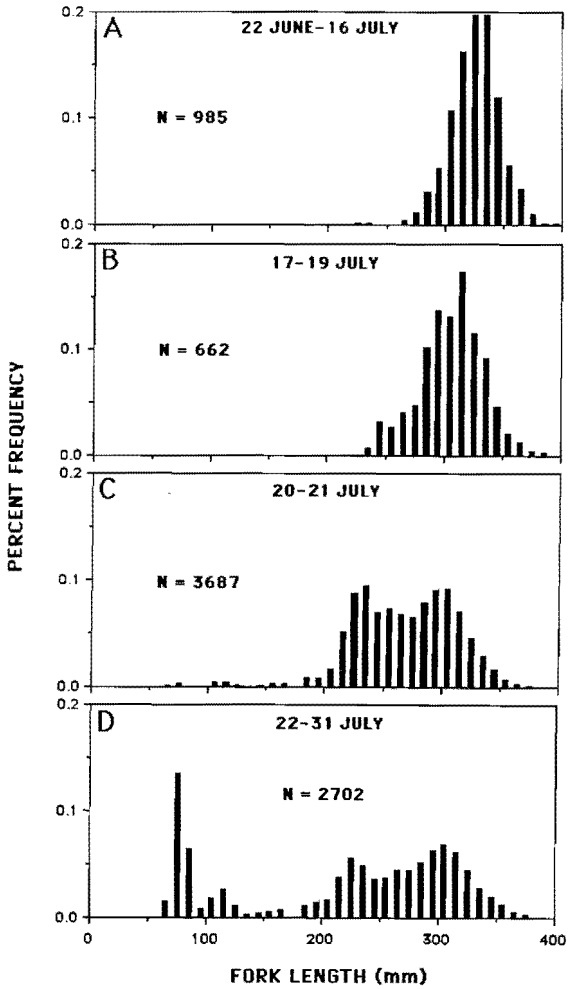

Figure 5. Length–frequency distributions for least cisco collected west of West Dock causeway during 22 June–31 July 1984.

0.568, $P = 0.001$; see Appendix A). There was no significant association between CPUE and salinity.

Groups 2, 3, and 4 also arrived west of the causeway during a period of westerly winds and generally increasing temperature (Fig. 6). Immediately upon the arrival of the last group, winds shifted to easterlies and salinity began to increase (Fig. 6A). CPUE for all size classes either declined or remained low after the onset of easterly winds. A major marine intrusion occurred during the last day of July, resulting in a drastic rise in salinity and a drop in temperature (Figs. 6A and 7A). After this event the only least cisco found west of West Dock for the remainder of the season were fish migrating back to the Colville River from Prudhoe Bay and a small contingent that milled about the Kuparuk Delta (Figs. 7B and C).

Spearman's Rank Correlation Analyses and Student's *t*-test were used to test among and between CPUE, water temperature, and salinity. Because surges in catch were of limited duration, we tested among variables for 6 days following initial increases in CPUE. The 6-day constraint encompassed periods of maximum catch activity for each size group: 18–23 July for Group 2, 20–25 July for Group 3, and 23–28 July for Group 4. Comparisons were made between data collected at barrier island nets (19, 23) and mainland nets (12, 15, 16, 17, 21, and 25) (Stations 20 and 24 were not fully operational). Nets 15 and 16 were included in the mainland group because of their close physical proximity to the mainland (Fig. 2) and because CPUEs were comparable to other mainland stations. Results are presented in Tables 1 and 2.

Group 2 least cisco were taken in substantial numbers inside of the barrier islands as well as along the main shore. It is not known if these fish were moving along the outside of the barrier islands since nets 14, 18, and 22 were not functional at this time. There were no significant differences in CPUE or temperature between the barrier island and mainland stations (Table 1). Salinity, however, was significantly higher at the barrier islands stations. There were no significant associations between CPUE and

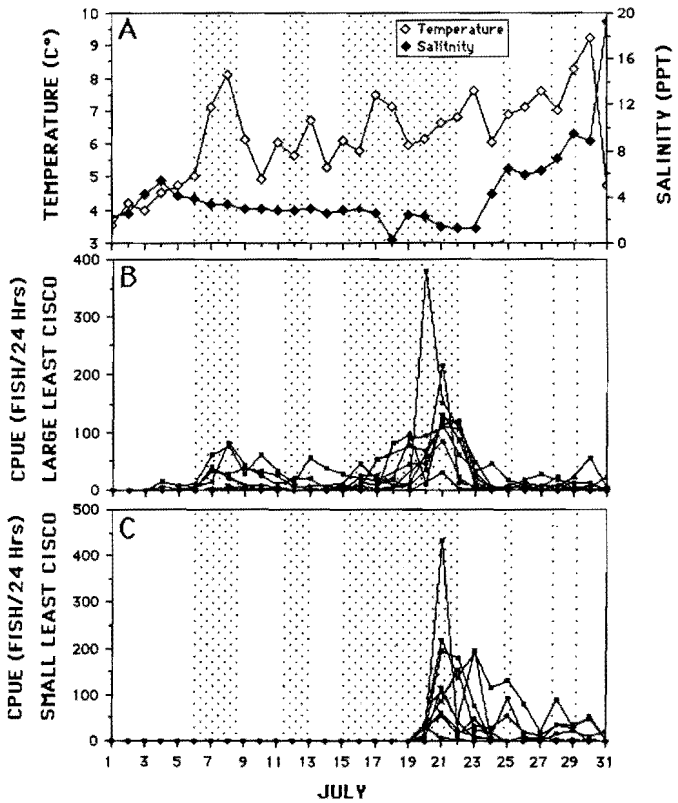

Figure 6. (A) Average surface salinity and average surface water temperature west of the causeway; CPUE for (B) large (≥250-mm) and (C) small (<250-mm) least cisco at individual fyke west of the causeway during 1–30 July 1984. Stippled areas denote periods of westerly winds and clear areas denote periods of easterly winds.

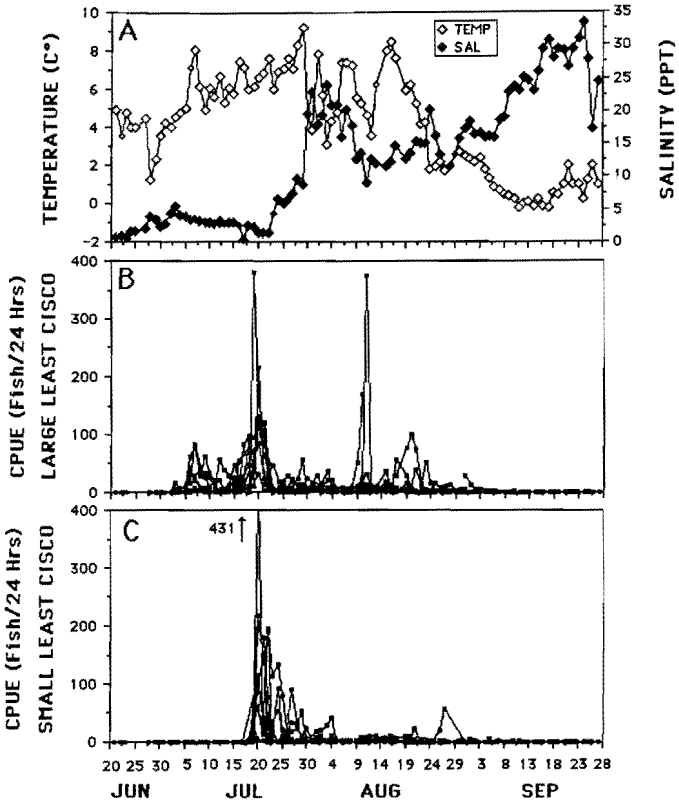

Figure 7. (A) Average surface salinity and average surface water temperature west of the causeway; CPUE for (B) large (≥250-mm) and (C) small (<250-mm) least cisco at individual fyke nets west of the causeway during 22 June–28 September 1984.

temperature or between CPUE and salinity (Table 2). Higher salinity at the barrier islands did not appear to deter Group 2 fish.

CPUE for Group 3 fish was significantly higher at the mainland stations, as was temperature. Salinity was significantly lower at the mainland stations. There was a positive association between temperature and CPUE, and there was a highly significant inverse association between salinity and CPUE. Results suggest that Group 3 moved

Table 1. Results of Student's *t*-tests comparing CPUE, temperature, and salinity among mainland and barrier island stations during the periods 18–23 July (≥250 mm), 20–25 July (120–249 mm), and 23–28 July (<120 mm). Dates correspond to periods of maximum catch activity west of the causeway for respective size classes.

CPUE	Temperature	Salinity
	Large least cisco (≥250 mm FL)	
$t = 0.592$ $P = 0.558$ df = 31	$t = 1.500$ $P = 0.143$ df = 31	$t = -5.000$ $P < 0.001$* (B > M) df = 30
	Small least cisco (120–249 mm FL)	
$t = 2.730$ $P = 0.009$* (M > B) df = 43	$t = 3.996$ $P < 0.001$* (M > B) df = 42	$t = -2.497$ $P = 0.017$* (B > M) df = 41
	Small least cisco (<120 mm FL)	
$t = 3.900$ $P < 0.001$* (M > B) df = 46	$t = 5.051$ $P < 0.001$* (M > B) df = 45	$t = -2.118$ $P = 0.042$* (B > M) df = 41

* Significant at ≤0.05 level. M = Mainland; Stations 12, 15, 16, 17, 21, and 25. B = Barrier island; Stations 19 and 23.

Table 2. Results of Spearman's rank correlation analysis comparing CPUE versus temperature and CPUE versus salinity for fyke nets west of the causeway during the periods 18–23 July (≥250 mm), 20–25 July (120–249 mm), and 23–28 July (<120 mm). Dates correspond to periods of maximum catch activity for respective size classes.

Large least cisco (≥250 mm FL)	Temperature vs. CPUE	$\rho = 0.014$ $P = 0.940$
	Salinity vs. CPUE	$\rho = 0.030$ $P = 0.871$
Small least cisco (120–249 mm FL)	Temperature vs. CPUE	$\rho = 0.304$ $P = 0.045$*
	Salinity vs. CPUE	$\rho = -0.618$ $P < 0.001$*
Small least cisco (<120 mm FL)	Temperature vs. CPUE	$\rho = 0.694$ $P < 0.001$*
	Salinity vs. CPUE	$\rho = -0.708$ $P < 0.001$*

* Significant at the $P < 0.05$ level.

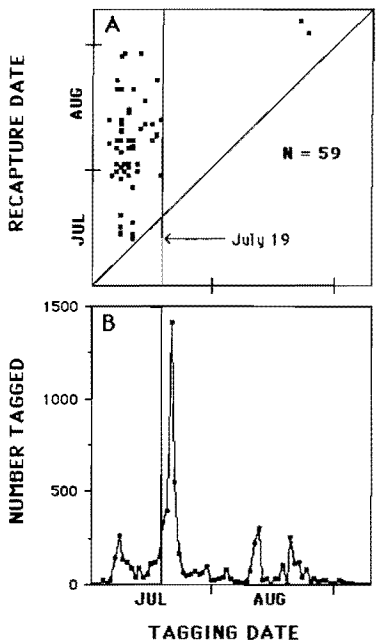

Figure 8. (A) Tagging and recapture dates for large (≥250-mm) least cisco marked west of the causeway and recaptured east of the causeway during 1984. (B) Total number of large least cisco marked west of the causeway by date during 1984.

along the mainland shore in response to higher temperatures and lower salinities.

Similarly, least cisco <120 mm (Group 4) showed a highly significant positive association with temperature and a negative association with salinity. Both CPUE and temperature were significantly higher at the mainland stations, while salinity was lower. The nearshore distribution of Group 4 least cisco may also have been in response to warmer, less saline waters.

The affinity for warmer, less saline water is believed to be partially responsible for the reduction in CPUE for small fish west of the causeway in late July. Easterly winds and the accompanying marine intrusion cause fish to retreat westward. Although we found no quantitative association between hydrography and catch for large least cisco, their disappearance after the major marine intrusion on 30 July implies an aversion to marine conditions. The permanent increase in salinity prevented them from approaching the eastern end of the lagoon system for the remainder of the season.

In summary, least cisco from the Colville River arrived in the study area abruptly and on different dates depending upon size: 7–8 July for Group 1, 18–19 July for Group 2, 22–23 July for Group 3, and 23 July for Group 4. All groups arrived in conjunction with westerly winds (easterly currents) and increasing temperatures. Individuals <250 mm tended to move along the mainland shore, possibly in response to warmer temperatures and lower salinities. Larger fish made greater use of the barrier island chain. Some portion of each group was able to circumvent West Dock and enter Prudhoe Bay. A major marine intrusion beginning on 31 July caused fish of all sizes to vacate waters west of West Dock for the remainder of the season.

Movement around West Dock causeway. West Dock influenced the alongshore migration of all size groups of least cisco in that fish generally began appearing in Prudhoe Bay at least a day after they first appeared west of the causeway. By itself, this does not necessarily mean that the overall eastward migration was halted. Mark–recapture data, however, suggest that many large least cisco belonging to Group 2 did not move into Prudhoe Bay.

Of 6,624 fish tagged west of the causeway, 59 were recaptured east of the causeway (Fig. 8). Except for two individuals marked and recaptured late in the season, all of the recaptured fish had been tagged west of the causeway prior to 19 July. For the 1,406 fish tagged prior to 19 July (Group 1), the 57 recaptures represent a return rate of 4.05 percent. Conversely, only two (0.04%) of the 5,218 fish marked after 18 July (predominantly Group 2) were recaptured in Prudhoe Bay. This latter group includes a large block of 2,697 fish tagged west of the causeway between 19 and 23 July, none of which were recovered in Prudhoe Bay. The 4.05 percent return rate for Group 1 was significantly ($\chi^2 = 109.38$, $P > 0.001$) higher than the 0 percent return rate for Group 2, which suggests that a greater proportion of Group 1 bypassed West Dock and entered Prudhoe Bay. (Statistical comparisons for this and all mark–recapture results required standardization of recapture efforts; Appendix A.) Several hypotheses were addressed that could account for the low number of Group 2 tag returns in Prudhoe Bay.

Hypothesis 1—Low recapture rates resulted from ex-

cessive mortality due to overcrowding in the fyke nets. This phenomenon would selectively remove marked fish from the population and lower the number of tag returns. Short-term mortality (96-hr) experiments have indicated a survival rate of about 95 percent for both tagged and untagged (large) least cisco; however, these studies have not considered size of catch as a test variable (Griffiths and Gallaway 1982; Critchlow 1983).

To determine if excessive net mortality occurred west of the causeway during 18–23 July, Colville River commercial fishery catches were analyzed for the presence of tagged least cisco. The fishery typically catches large numbers of tagged fish each year. Because commercial nets are selective for fish between 280 and 400 mm (mode = 300–310 mm), recapture rates were adjusted to compensate for size discrepancies (Appendix B).

Size of catch was defined as the total number of large fish (>250 mm) taken by individual nets. Although all sizes of fish are collected, we estimated that large fish constitute the greatest proportion of biomass. Total numbers were calculated regardless of species and included least cisco, Arctic cisco, char, broad whitefish (*Coregonus nasus*), humpback whitefish (*C. pidschian*), and pink salmon (*Oncorhynchus gorbuscha*). Individual daily fyke-net catches were grouped into one of three categories: <50 fish/day, 50–100 fish/day, and >100 fish/day. For each size category, recapture rates at the Colville fishery (adjusted for length) were computed.

Results revealed no significant difference ($\chi^2 = 3.1$, $P > 0.10$) in tag returns among the three categories and imply that mortality was not a function of size of catch. Thus, excessive net mortality did not appear to be the cause of low return rates in Prudhoe Bay. Uniformly high mortality throughout the 1984 study can be discounted because many return rates were substantial: 4.83 percent of the fish tagged in Prudhoe Bay were recovered in the study area, and 4.05 percent of the fish tagged west of the causeway prior to 19 July were recovered in Prudhoe Bay.

Hypothesis 2—Tagging efforts west of the causeway marked only a tiny fraction of Group 2 due to gear saturation or the use of too few nets. Upon release, marked fish became an insignificant proportion of the population and failed to appear in Prudhoe Bay fyke nets. If the unmarked portion of Group 2 fish was large enough to suppress recapture rates in Prudhoe Bay, it should have equally suppressed the recapture rates of Group 1. However, 51 of 57 Group 1 fish were recaptured in Prudhoe Bay after the arrival of Group 2 (Fig. 8).

Hypothesis 3—A large proportion of Group 2 fish bypassed West Dock but overshot Prudhoe Bay and moved into the Sag Delta or beyond. This hypothesis is questionable since there was no indication of a major return migration later in the season. Of 2,697 fish tagged west of the causeway from 18 to 23 July, 15 were recaptured throughout the entire study area. Eight were recovered within 4 days and are not relevant to long-term movement patterns. The remaining seven recaptures (0.26% return rate) provided little evidence to indicate a major return migration back to overwintering grounds in the Colville River.

Hypothesis 4—The most likely case is that few large least cisco passed east of West Dock after 18 July. From 18 to 21 July, when CPUE west of the causeway was increasing 80 percent (855) of the catch at barrier island Stations 15, 19, and 23 occurred in the west side of the fyke nets. When CPUE west of the causeway began dropping on 22 July, 87 percent (236) of the catch occurred on the east side of the nets. (Nets outside the barrier islands were not operational at this time.) This shift indicates a reversal in migratory direction from east to west. Except for mid-lagoon Station 16, the remaining stations west of the causeway continued to catch most large fish on their western side.

The apparent reversal along the barrier islands coincided with a marine water intrusion east of West Dock. On 20 July, when fish were moving into waters west of the causeway, Station 13, located at the eastern base of West Dock, registered a sharp increase in salinity from 1.8 to 8.8 ppt and a drop in temperature from 5 to 2°C. The marine intrusion was also reported along the eastern face of the causeway (Savoie and Wilson 1986). The marine intrusion became evident at Station 5 on 21 July, when salinity increased from 0.6 to 9.3 ppt and temperature dropped from 6 to 4°C. Smaller increases in salinity were recorded at Stations 2, 3, 6, and 7 on 22 July. The smaller change at these stations probably reflected dilution of the marine water as it mixed with low-salinity water in Prudhoe Bay.

While the marine intrusion in western Prudhoe Bay was short-lived and its total extent unknown, it occurred when Group 2 least cisco were moving into the area from the west. The presence of a sharp interface in northwestern Prudhoe Bay could have diverted fish to the west (change in direction along the barrier islands). The decline in catch west of the causeway after 23 July reflected a westward exodus from the study area.

Although data suggest that few Group 2 fish moved east of West Dock, enough individuals made it to noticeably shift length–frequency distributions in Prudhoe Bay. Prior to the arrival of Group 2 length–frequency distributions on both sides of the causeway were modal at 310–330 mm (Fig. 9). After the arrival of Group 2 there was an equivalent downshift in the modes on both sides of the causeway. Data indicate that Group 2 fish did bypass West Dock.

This apparent paradox is likely related to the numerical superiority of Group 2 over Group 1. On 7–9 July, when Group 1 was moving through the lagoon system, their distribution was restricted to mainland shore Stations 12, 15, 17, 21, and 25. A comparison of peak catch rates at these stations showed CPUE levels for Group 2 (19–21 July) to be two to five times higher. Further, Group 2

was not confined to the mainland shore stations. Station 23 alone caught more large least cisco on 20–21 July (N = 568) than all of the lagoon nets combined during 4–9 July (N = 560). Numerically, Group 2 was much larger than Group 1. Thus, only a small portion of Group 2 may have been sufficient to shift the length–frequency distribution of fish in Prudhoe Bay.

Catch rates for small least cisco in Prudhoe Bay never reached levels observed west of the causeway and suggest that few fish resided in Prudhoe Bay (Figs. 4C and D). Mark–recapture data support this contention. Of the 2,479 individuals marked west of the causeway, primarily from 21–24 July, only four (0.12%) were recaptured east of the causeway.

Low return rates are not completely due to marking mortality. Assuming a mortality rate of 35 percent, the highest recorded for a freeze-branding test on least cisco (Critchlow 1983; Moulton et al. 1986), the recapture rate for fish marked west of the causeway and recaptured east of the causeway is still only 0.19 percent. By comparison, of 1,060 small fish marked in Prudhoe Bay, 47 (4.44%) were recaptured in Prudhoe Bay. The fishing effort in Prudhoe Bay was sufficient to recapture a relatively good percentage of branded fish, provided the fish were residing in the bay.

In summary, the first group of large least cisco that arrived in the study area in early July apparently moved east of West Dock without any problem. Immediately after the arrival of Groups 2, 3, and 4 later in the season, a shift to easterly winds resulted in marine intrusions that caused fish that had not passed east of the causeway to retreat westward. The intrusion was permanent and fish in the lagoon system did not approach the causeway for the remainder of the season.

East of causeway. CPUE (Fig. 4B) and mark–recapture data indicate that large least cisco remained in Prudhoe Bay until the end of August. Of the 7,622 fish tagged in Prudhoe Bay, 270 (3.54%) were recaptured east of the causeway. It was not until the last week in August that tag returns and CPUE simultaneously dropped to negligible levels.

Some large least cisco that moved east of West Dock did not travel down the eastern face of the causeway. During 24–30 July, CPUE in Prudhoe Bay increased after CPUE west of West Dock decreased (Figs. 4A and B). Catch at western Prudhoe Bay Stations 5, 6, 8, and 13 (61.8 fish/net/day) was four times higher than for eastern/central bay Stations 1, 2, 3, 4, and 27 (15.1 fish/net/day). The shift in CPUE suggests movement from the lagoon into western Prudhoe Bay. However, the events were separated by 48 hours. From 19 to 30 July, 12 (nine recaptures adjusted for equal recapture effort; see Appendix A) of 494 fish tagged in eastern Prudhoe Bay were recovered on the western side of the bay. Conversely, only one of the 1,748 fish marked in western Prudhoe Bay was recovered at the eastern bay stations. The difference in recapture rates was highly significant ($\chi^2 = 40.07$, $P < 0.001$), indicating movement from east to west within Prudhoe Bay. The 48-hour gap between the disappearance of fish in the lagoon and their appearance in western Prudhoe Bay, coupled with tag data, indicates that fish rounded West Dock, moved undetected across the middle of Prudhoe Bay to the Sag Delta, then moved back into Prudhoe Bay from the east.

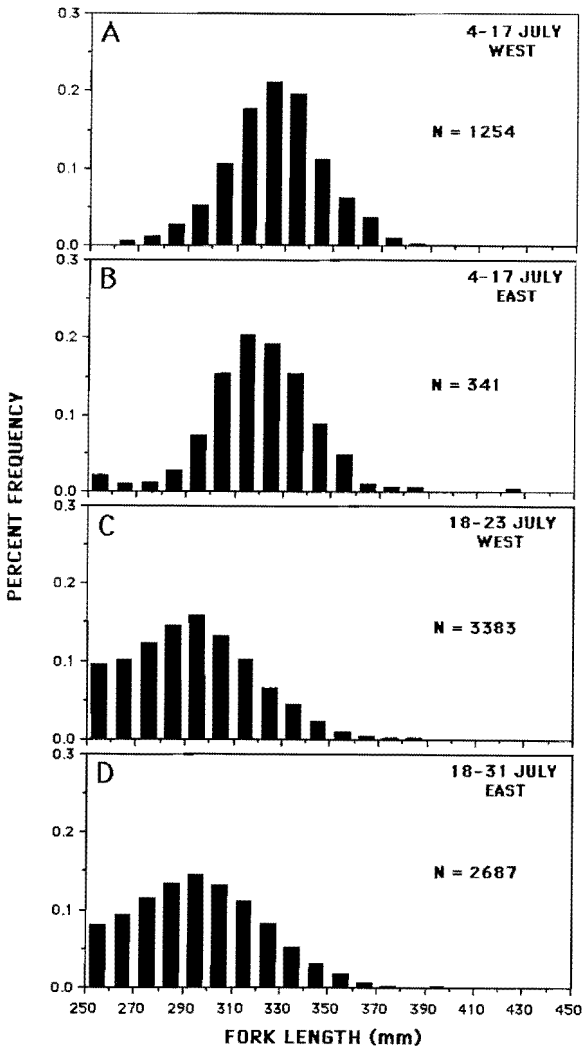

Figure 9. Length–frequency distributions for large (≥250-mm) least cisco collected by fyke net (A) west and (B) east of the causeway during 4–17 July, (C) west of the causeway during 18–23 July, and (D) east of the causeway during 18–31 July.

The move from east to west Prudhoe Bay occurred during a period of easterly winds and increased water temperature (Figs. 10A and B). Temperature increases resulted from the westward deflection of the Sag plume.

CPUE declined throughout Prudhoe Bay on 30–31 July in conjunction with a marine water intrusion. The intrusion was caused by a shift to westerly winds that caused marine water that had accumulated around West Dock to enter Prudhoe Bay from the northwest. The effect of the Sag plume was also negated because of deflection away

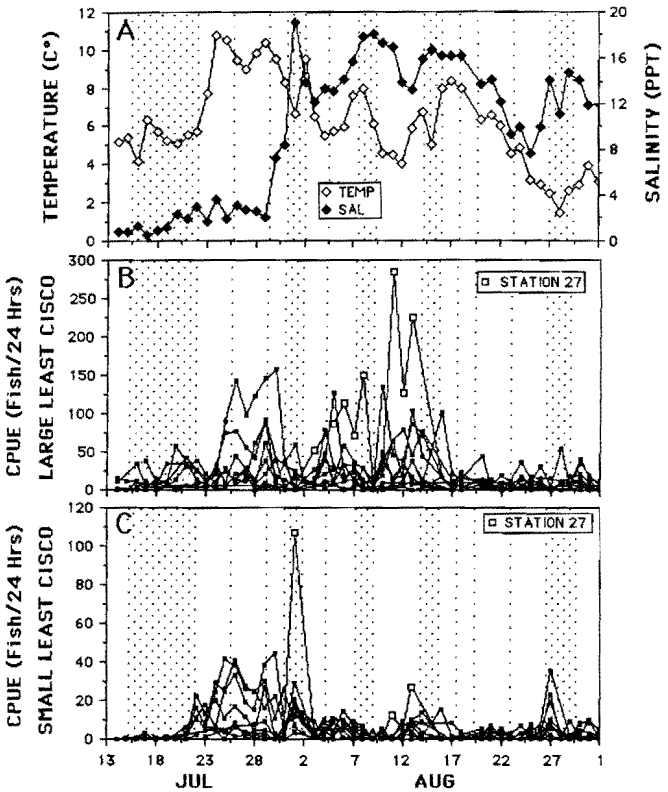

Figure 10. (A) Average surface salinity and average surface water temperature; CPUE for (B) large (≥250-mm) and (C) small (<250-mm) least cisco at individual fyke nets west of the causeway during 1–30 July 1984. Stippled areas denote periods of westerly winds and clear areas denote periods of easterly winds.

from Prudhoe Bay. The front apparently caused fish to retreat to the Sag Delta since once the intrusion had run its course, the highest catches occurred at Station 27, located at the eastern edge of the Sag Delta (Fig. 10B). In addition, from 1 to 13 August, 24 fish that had been tagged in other parts of Prudhoe Bay were recaptured at Station 27.

CPUE for large least cisco declined sharply after 14 August, and by September catch was negligible. Fish had left the area and returned to the Colville River.

Catch patterns for small least cisco in Prudhoe Bay were similar to those for large fish. A decline in CPUE occurred during the 31 July marine intrusion (Fig. 10C). Although catches dropped throughout the bay, there was a sharp peak at net 27 on 1 August, which again suggests a retreat toward the Sag River.

From 2 August onward, CPUE at the Prudhoe Bay stations generally remained below 20 fish/net/day. There were notable peaks in catch around 13 and 27 August that were associated with a westward migration out of Prudhoe Bay.

Westward migration. Large least cisco left Prudhoe Bay by moving around the tip of the causeway and continuing west along the outside of Stump Island. From late July to early September, Station 14 (located on the seaward side of Stump Island) had the highest average catch (30 fish/day) of any station west of the causeway. Over 90 percent of all fish were collected on the east side of the net, implying movement from east to west. Of the 104 large least cisco tagged in Prudhoe Bay and recaptured west of the causeway, 59 (57%) were recovered at Station 14. Movement through the breach was not possible because this avenue was entirely blocked by nets.

Large least cisco were also taken at Stations 25 and 21 during midseason; however, much of this catch appeared unrelated to fish migrating through the area from Prudhoe Bay. During late July to early September, tagged fish from Prudhoe Bay comprised only 0.86 and 1.75 percent of the total catch at Stations 21 and 25, respectively. This compares with a range of 2.23–18.7 percent for the other stations west of the causeway. A greater portion of the catch at Stations 21 and 25 was not associated with fish of Prudhoe Bay origin. Fish may have congregated near the Kuparuk Delta in response to higher temperatures and lower salinities.

Data from other stations west of the causeway were insufficient to determine the route of migration once fish moved west of Station 14.

The catch of small least cisco west of the causeway suggests a scenario similar to that for large fish. Although only 669 fish were taken after 31 July (Fig. 4C), 67.7 percent were caught at Stations 14 (N = 117), 21 (N = 113), and 25 (N = 223). Mark–recapture data were inconclusive as only four (0.38%) of the 1,058 small least cisco branded in Prudhoe Bay were recaptured west of the causeway and only one of these at Station 14.

Arctic Cisco

Seasonal catch patterns for large Arctic cisco were similar to those for least cisco. Catch began abruptly west of the causeway on 3 July as fish moved in from the Colville River (Fig. 11A). Spikes in CPUE did not become evident in Prudhoe Bay until after these fish moved past West Dock (Fig. 11B). Catch declined late in the summer, indicating that many fish had left the area. Residual catch was noted in Prudhoe Bay late in the season and may reflect a few large fish overwintering in the Sag Delta. There was also some nominal catch very early in the season.

In contrast, small Arctic cisco were abundant in Prudhoe Bay the day sampling began on 22 June (Fig. 11D). CPUE was also notably higher in Prudhoe Bay throughout the season (Figs. 11C and D). Both trends reflect overwintering in the Sag Delta. The large surge in CPUE in late August is believed to represent small fish converging on the Sag Delta prior to feeze-up (Fig. 11D).

Eastward migration. The arrival of progressively smaller size classes of large Arctic cisco was evident from shifts in length–frequency distributions. From 22 June to

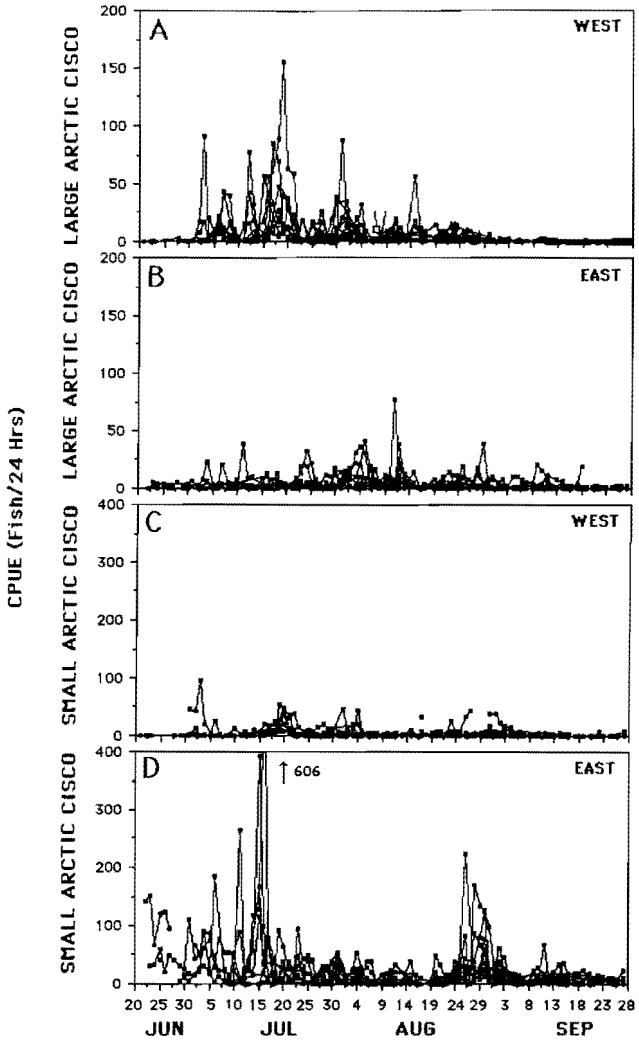

Figure 11. CPUE for large (≥250-mm) and small (<250-mm) Arctic cisco at individual fyke nets located (A, C) west and (B, D) east of the causeway during 22 June–28 September 1984.

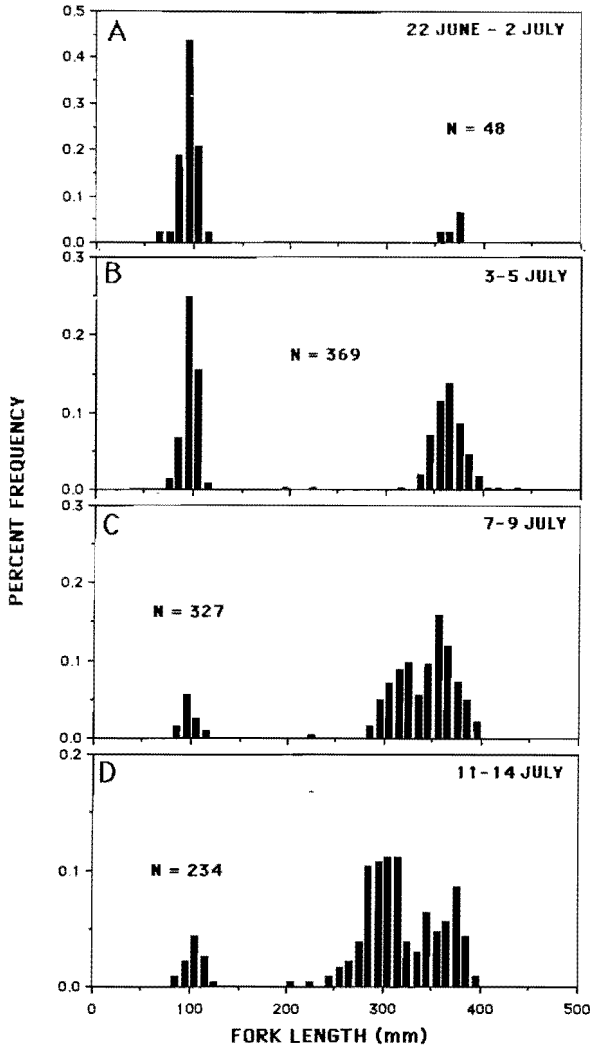

Figure 12. Length–frequency distributions for Arctic cisco collected west of the causeway during 22 June–14 July 1984.

2 July, catch west of the causeway consisted primarily of a 90–100-mm cohort (Fig. 12A). These smaller fish may have migrated westward from the Sag Delta since their length distribution is consistent with a dominant cohort observed east of West Dock. They might also represent a small contingent that overwintered in the Kuparuk Delta.

Three successive time periods saw shifts in the length frequency west of the causeway. A strong mode at 360–370 mm became apparent during 3–5 July (Fig. 12B) and was accompanied by a large increase in CPUE (Fig. 11A). A second mode at 320–330 mm appeared during 7–9 July (Fig. 12C). The lower mode flattened and centered about 290–300 mm during 11–14 July (Fig. 12D). These shifts imply an influx of increasingly smaller fish. Another increase in CPUE on 15–23 July resulted in a strong mode at 240–250 mm (Fig. 13A).

During 2–23 July, there was a significant positive association (Spearman's Rank Correlation Analysis; $\rho = 0.517$, $P = 0.014$) between average CPUE of large Arctic cisco and average temperature at fyke nets west of the causeway (Fig. 14). CPUE on 3 July was classified as an outlier and was not included in the analysis. Virtually all the 3 July catch was at Station 21 and was accompanied by a 2°C increase in temperature. This thermal increase was considerable given the range of temperatures at the time, but did not appreciably alter average temperature. Station 21 increased average CPUE by 400 percent.

The temperature relationship is consistent with the fact that most of the surges in CPUE occurred during periods of west winds (Fig. 15). Fish arrived in conjunction with the westward flowing warm-water plume.

CPUE and hydrographic data suggest fish belonging to the 240–250-mm mode size class may have originated from the pool available in Prudhoe Bay and not from the Colville River. Despite the statistically significant correlation during 2–23 July, the relationship between CPUE and temperature began to break down during 18–23 July

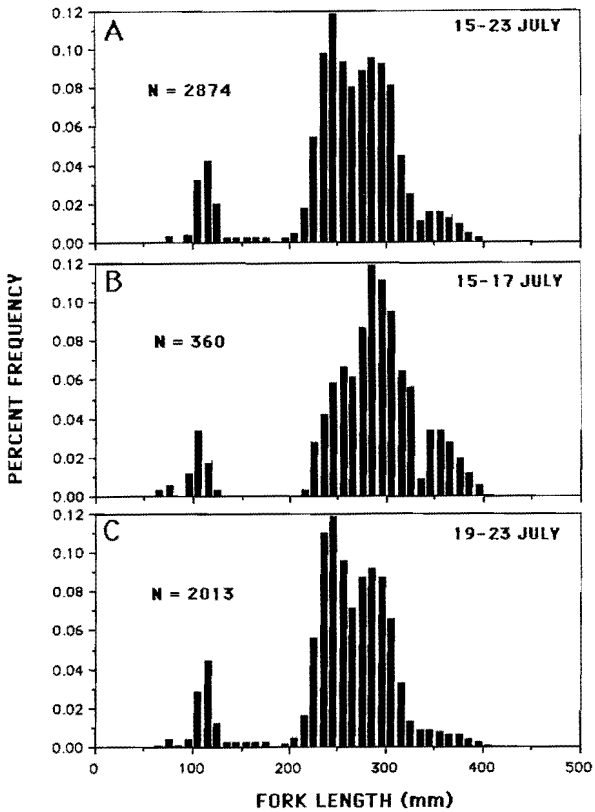

Figure 13. Length–frequency distributions for Arctic cisco collected west of the causeway during 15–23 July 1984.

(Fig. 14). A shift in the dominant mode prior to 18 July (Fig. 13B) and afterwards (Fig. 13C) suggests that the arrival of large numbers of fish <250 mm coincided with the breakdown in association. This size class was the dominant group overwintering in the Sag River. Fish moving west around the causeway would have to move onshore in order to be detected by the lagoon nets. This onshore movement would be out of synchrony with the east–west movement of Colville River fish and with an east–west oscillating environment. This may have resulted in the breakdown in association between CPUE and temperature.

Further comparisons of CPUE versus local hydrography west of the causeway were precluded by the massive marine water intrusion at the end of July that lowered overall catch west of West Dock. There were localized surges in CPUE of large Arctic cisco to mid-July levels on 30–31 July and 15 August (Fig. 11A), but Station 14 was by far the most productive net during the latter half of the season. Its predominance suggests that much of the activity west of the causeway in August was associated with westward migration out of Prudhoe Bay.

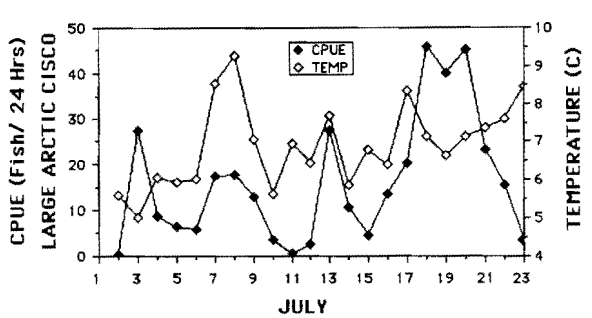

Figure 14. Average CPUE for large (≥250-mm) Arctic cisco and average surface water temperature west of the causeway during 2–23 July 1984.

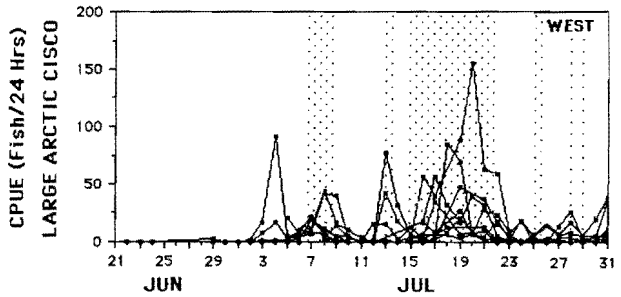

Figure 15. CPUE for large (≥250-mm) Arctic cisco west of the causeway during 22 June–31 July 1984. Stippled areas denote periods of westerly winds and clear areas denote periods of easterly winds.

Movement around West Dock causeway. Few Arctic cisco >300 mm were caught in Prudhoe Bay in 1984 despite the fact that at least two size-groups with modes >300 mm arrived west of the causeway on 3–5 July (Fig. 12B) and 7–9 July (Fig. 12C).

Of 2,168 fish tagged west of the causeway in July, seven (0.32%) were recovered in Prudhoe Bay. Only nine (0.70%) of the 1,988 large Arctic cisco tagged east of the causeway were recovered east of the causeway. Poor return rates for large Arctic cisco were a problem that plagued several of the Prudhoe Bay studies.

The absence of specific size cohorts and low tag return rates for large Arctic cisco in Prudhoe Bay do not imply blocked alongshore migration as readily as they might for least cisco. Unlike least cisco, large Arctic cisco range along the entire Beaufort Sea coast during the open-water season (Kendel et al. 1975; Griffiths et al. 1977; Griffiths 1983; Schmidt et al. 1983; Moulton et al. 1986). Low numbers of fish in Prudhoe Bay may indicate that fish continued to migrate along the coast. In addition, many of the large Arctic cisco that move into the study area may continue migrating eastward to Canadian waters on their return spawning migration. This would be particularly likely for larger individuals.

East of causeway. Reaction to the 31 July–2 August marine intrusion in Prudhoe Bay was not evident since CPUE for large Arctic cisco had diminished prior to the event (Fig. 16B). From 31 July to 8 August, CPUE was greatest at Stations 2 and 3, located in the middle of the bay at Gull Island. These data could reflect continued migration into Prudhoe Bay, the early stages of a migration out of Prudhoe Bay, or an onshore/offshore distri-

bution in response to hydrographic conditions. We found no clear evidence to clarify a cause and effect mechanism.

There were some isolated spikes in CPUE at several Prudhoe Bay nets in late August and early September but most of the catch activity declined after 12 August as fish left the area (Figs. 11A and B).

Most of the catch activity for small Arctic cisco in Prudhoe Bay occurred either early or late in the summer (Fig. 11D). There was a relative lack of activity between 18 July and 24 August. Movement patterns prior to 18 July are difficult to assess because many stations were not operational: Station 13 became operational on 14 July, Stations 5 and 6 on 17 July, Station 2 on 23 July, Station 3 on 28 July, and Station 7 on 31 July. Thus, much of the early season action in Prudhoe Bay had ended by the time a reasonably complete complement of nets had become operational.

The low levels of CPUE during midseason would indicate that many small fish were not residing in Prudhoe Bay. Although some fish did move west of the causeway, the generally low catch rates suggest that these fish did not constitute the bulk of the Sag population (Fig. 11C). It also seems unlikely that fish migrated west of the lagoon sampling grid early in the season since the resurgence in Prudhoe Bay catch in late August/early September was unaccompanied by increased catch west of the causeway. Movement east of the study area would have gone undetected.

Late season surges in CPUE were concentrated in eastern Prudhoe Bay. Eastern bay stations (1–4, 27) averaged 48.2 fish/net/day compared to 21.9 for western bay stations (5–8, 13). Results reflect fish returning to overwintering grounds in the Sag Delta.

Mark–recapture data also indicate that many fish remained east of the causeway. Of the 6,488 small Arctic cisco freeze-branded in Prudhoe Bay, 137 (2.11%) were recaptured east of the causeway with readable brands. This rate is probably an underestimate since 104 fish were captured with unreadable brands. By comparison, only six (0.09%) marked fish were recaptured west of the causeway during the entire season.

The generally higher CPUE in Prudhoe Bay does not necessarily indicate that West Dock prevented small Arctic cisco from moving into the barrier island lagoons. During the period 14–27 July, average CPUE was 92, 52, 40, and 3 fish/day at Stations 1, 4, 8, and 13, respectively. These stations reflect a horizontal cross section of events in Prudhoe Bay (Fig. 2). Although the highest seasonal levels of CPUE were being recorded in Prudhoe Bay, the east–west gradient in catch was sharp enough such that relatively few fish were being caught immediately east of West Dock. The westward distribution of small Arctic cisco appeared to have essentially terminated before reaching West Dock causeway.

Westward migration. Large Arctic cisco also exited Prudhoe Bay by moving around the causeway and west

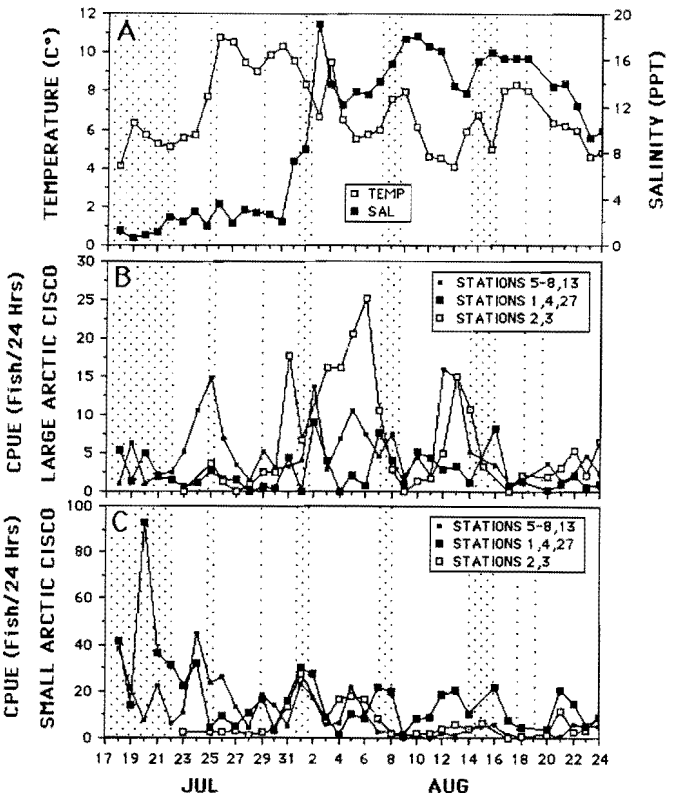

Figure 16. (A) Average surface salinity and average surface water temperature east of the causeway; CPUE for (B) large (≥250-mm) and (C) small (<250-mm) Arctic cisco at station groups east of the causeway during 17 July–24 August 1984. Stippled areas denote periods of westerly winds and clear areas denote periods of easterly winds.

along the outside of the barrier islands. Station 14 accounted for over 50 percent of the fish taken west of the causeway during 5 August–3 September (period of operation). Over 88 percent of these fish were collected on the east side of the net, implying westward movement. Only five (0.25%) of the 1,988 large Arctic cisco tagged in Prudhoe Bay were recovered west of the causeway; however, four of these were taken at net 14.

The highest seasonal catches of small Arctic cisco west of the causeway were at nets 14, 21, and 25. Excluding the 16–23 July catch, these three nets accounted for 85 percent (N = 1,360) of all small Arctic cisco taken west of the causeway. Results are similar to those for least cisco, in which a small contingent of fish milled around the Kuparuk Delta, presumably in response to lower salinities and warmer temperatures. The high catch at Station 14 again suggests movement westward around the causeway. Only five (0.08%) of 6,488 small fish marked in Prudhoe Bay were recovered west of the causeway, but three of them were taken at Station 14. Given the sharp disparity in peak levels of CPUE and the poor return rate of marked fish, the small Arctic cisco taken west of the causeway may have been only a small portion of the Prudhoe Bay population.

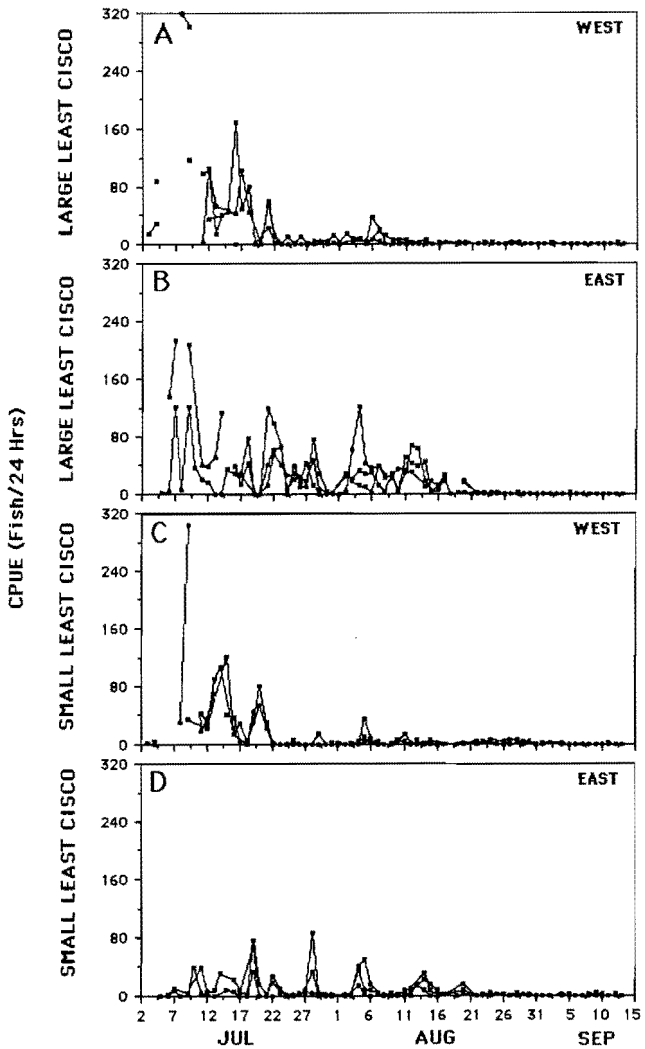

Figure 17. CPUE for large (≥250-mm) and small (<250-mm) least cisco at individual fyke nets located (A, C) west and (B, D) east of the causeway during 2 July–13 September 1981.

Small Arctic cisco were most abundant at Station 14 during the end of August and early September. Whether these fish were members of the Sag River population that had not yet retired to overwintering areas or were fish that dispersed westward from the Colville River is unknown.

1981

The 1981 study was conducted from 3 July to 13 September and employed seven fyke nets (Fig. 2). Gill nets were used on an intermittent basis. Unlike later surveys, lengths for small fish were not recorded on a daily basis; however, small fish were distinguishable from large fish because of mark–recapture efforts: small fish were fin-clipped and large fish were Floy-tagged. Lengths were recorded for large fish.

Fin-clipping proved to be a less informative marking technique than freeze-branding. The latter method identified both the date and station at which a fish was marked. Fin-clipping merely identified the side of the causeway on which the fish was marked.

Least Cisco

Seasonal catch data indicated that least cisco were in the study area when sampling began on 3 July (Fig. 17). Data also show that small fish arrived in the study area at least 2 weeks earlier than in 1984. CPUE for all size classes dropped to nominal levels by mid-August, indicating that fish had returned to the Colville River.

Eastward migration. Length–frequency distributions for July indicated the presence of at least two size cohorts of large fish: 320–330- and 280–290-mm modes. These same cohorts were also observed in Prudhoe Bay.

Seasonal catch for small least cisco west of the causeway was characterized by three peaks of progressively smaller magnitude centered about 9, 14, and 20 July (Fig. 18D). Spearman's Rank Correlation Analysis yielded a significant ($\rho = 0.725$, $P = 0.008$) positive association between daily average temperature and CPUE for the period 11–22 July (data were inconsistent prior to 11 July). There was no significant association between CPUE and salinity. Both water temperature and CPUE generally increased with westerly winds and decreased with easterly winds (Figs. 18A and B). Small fish again appeared to be responding to wind-driven fluctuations in water temperature and/or current.

Unlike 1984, CPUE for large fish appeared to be independent of wind and hydrographic conditions (Fig. 18C). Once continuous sampling began, some of the largest spikes in CPUE occurred during a period of easterly winds when temperature was approaching an interim low. For the period 11–22 July, there were no significant associations between CPUE and temperature or between CPUE and average salinity.

Few large or small least cisco were taken west of the causeway after 21 July (Figs. 17A and C). The first major marine intrusion of the summer began on 20 July, and by 25 July lagoon waters neared 30 ppt and temperatures dropped below 6°C (Figs. 18A and B). Fish that had not moved east of the causeway apparently retreated westward and they did not return in appreciable numbers.

Movement around West Dock causeway. Recapture rates for least cisco marked west of the causeway were poor for both size groups. Of 2,489 large fish tagged west of the causeway, nine were recaptured in the study area—three (0.1%) east of the causeway and six (0.2%) to the west. Only two (0.1%) of the 1,220 small fish fin-clipped west of the causeway were recovered—one east and one west of West Dock.

Mark–recapture results were similar to 1984 in that few fish marked west of the causeway were recovered in Prudhoe Bay. However, the lack of recoveries in 1981 is less meaningful because the sampling effort was much more

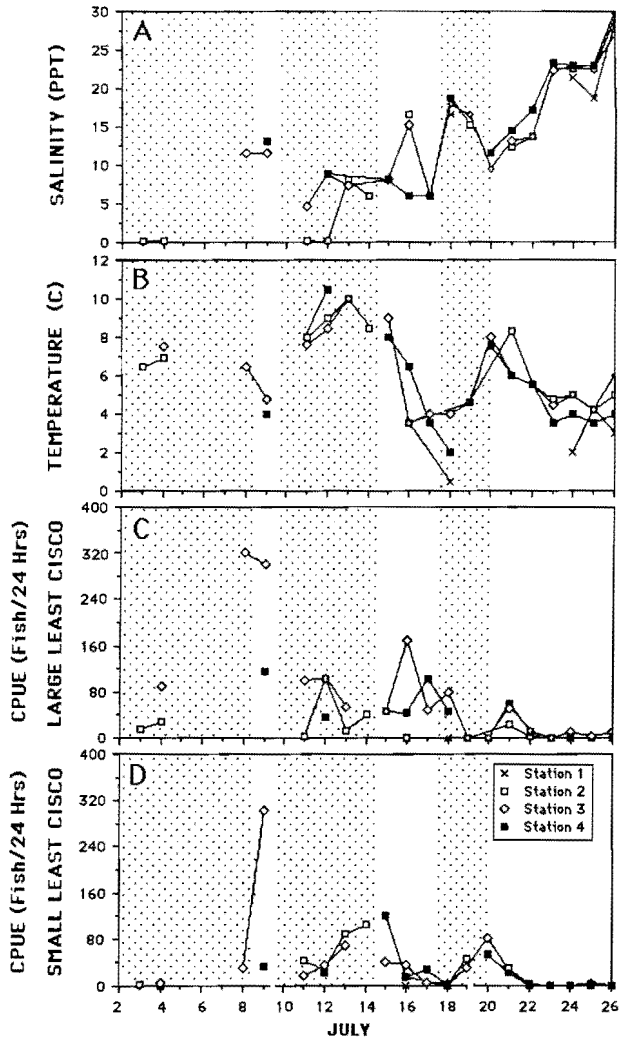

Figure 18. (A) Surface salinities; (B) surface water temperatures; CPUE for (C) large (≥250-mm) and (D) small (<250-mm) least cisco at fyke nets located west of the causeway during 3–26 July 1981. Stippled areas denote periods of westerly winds and clear areas denote periods of easterly winds.

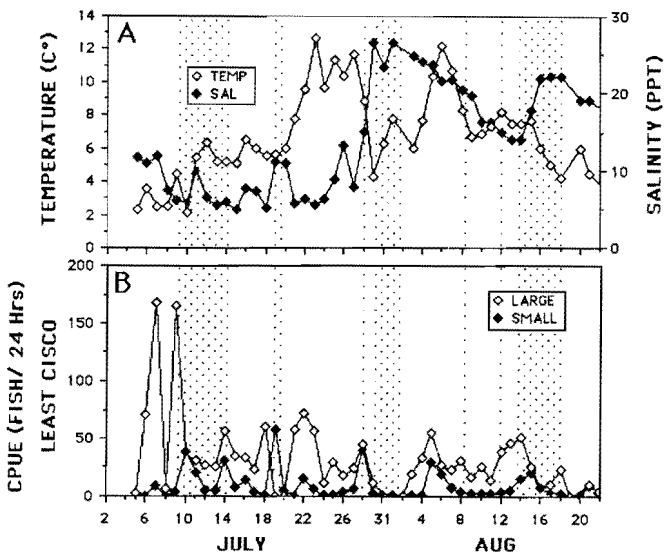

Figure 19. (A) Average surface salinity and average surface water temperature; (B) CPUE for large (≥250-mm) and small (<250-mm) least cisco east of the causeway during 5 July–22 August 1981. Stippled areas denote periods of westerly winds and clear areas denote periods of easterly winds.

restricted than in 1984 (Fig. 2). It is conceivable that fish dispersed east of the causeway but that many avoided recapture because of the small number of sampling stations. In addition, many fish may have migrated into Prudhoe Bay before continuous sampling commenced on 11 July.

With the exception of catches at Station 3 on 8–9 July, peak levels of CPUE for both large and small least cisco were not dramatically different based upon side of causeway (Fig. 17). In addition, the 320–330- and 280–290-mm cohorts detected west of the causeway were also present in Prudhoe Bay. This, coupled with insufficient mark–recapture data, limited spatial scope of sampling, and the late start-up date, precludes speculation that least cisco were unsuccessful in bypassing West Dock causeway and residing in Prudhoe Bay during 1981.

East of causeway. Of the 3,668 large fish tagged in Prudhoe Bay, 59 (1.6%) were recaptured east of the causeway. The recapture rate was half that recorded in 1984, but this again may be a function of differing effort (703 net-days in 1984 versus 180 net-days in 1981). Given the limited number of stations, the 1.6 percent return rate indicates residency in Prudhoe Bay.

Only seven (0.7%) of 996 small fish marked in Prudhoe Bay were recovered, and all were taken east of the causeway. Senior field supervisors noted that fish recaptured later in the season had partially damaged pelvic fins, and field personnel could not be certain whether this damage was due to natural circumstances or the result of partial regeneration of an earlier clip (W. B. Griffiths, pers. comm. 1985). These fish were not classified as recaptures, which may have contributed to lower return rates. Limited spatial effort and marking mortality may also have been contributing factors.

Both large and small fish appeared to react strongly to the season's first major marine intrusion on 28–29 July. The onset of westerly winds after a period of easterly winds pushed marine water into Prudhoe Bay from the northeast. This caused a dramatic increase in salinity and a decrease in temperature (Fig. 19A). CPUE for both size classes dropped to negligible levels over the next 72 hours (Fig. 19B). This trend is consistent with 1984 when fish retreated toward the Sag Delta under similar circumstances. A similar retreat may have occurred on 9 July when easterly winds and a 2°C drop in temperature also marked a big decline in CPUE for large fish (Fig. 19B).

CPUE for both size groups declined to negligible levels after 16 August, indicating that fish had left the study area (Figs. 17B and D).

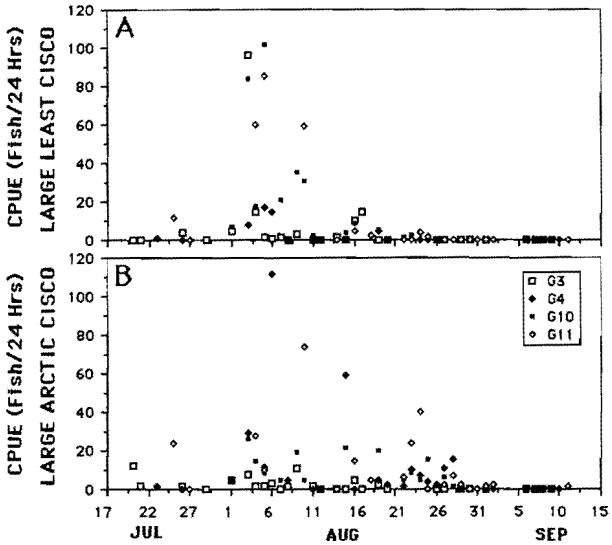

Figure 20. CPUE for (A) large (≥250-mm) least cisco and (B) large Arctic cisco at gill nets located around West Dock causeway during 17 July–15 September 1981. Nets were located at the causeway's tip (G10), breach (G3), western face (G4), and eastern face (G11).

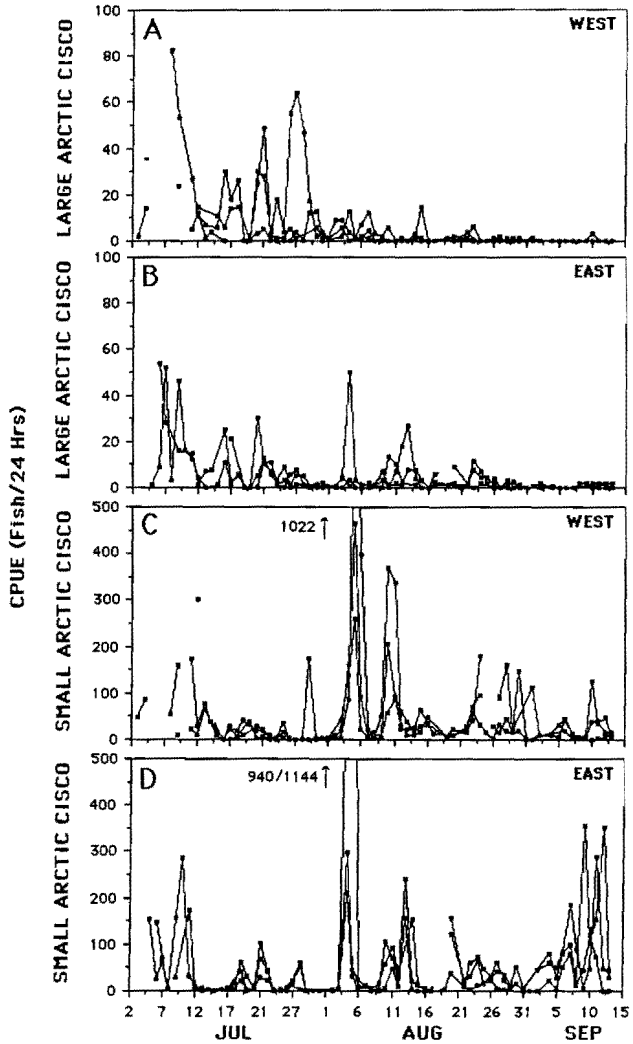

Figure 21. CPUE for large (≥250-mm) and small (<250-mm) Arctic cisco at individual fyke nets located (A, C) west and (B, D) east of the causeway during 3 July–13 September 1981.

Westward migration. Migration out of Prudhoe Bay apparently began in early August. On 3–6 August, CPUE for large and small fish increased on both sides of the causeway, with peak catches first occurring in Prudhoe Bay (Fig. 17). Increased CPUE was recorded at all nets west of the causeway, including Station 1 located at the western tip of Stump Island (Fig. 2). Station 1 only caught 92 least cisco during the entire season, but 44 were taken on 4–5 July. The distinguishing feature of Station 1 is that it was the only net that could have detected movement along the outside of the barrier islands. Gill nets (150 × 8 ft, 5-in stretched mesh) operating near West Dock causeway from 20 July to 11 September also indicated activity during 3–10 August (Fig. 20A). A return migration was supported by the fact that of 12 large fish tagged in Prudhoe Bay and recaptured in either gill nets or western fyke nets, seven were taken between 3 and 10 August.

The 3–10 August period was also dominated by easterly winds that caused temperature increases at stations east and west of the causeway. This effect was due to westward deflection of the Sag plume. Since this period marked the major exodus of least cisco, it is likely that fish may have been aided in moving around West Dock by the warm-water plume.

Arctic Cisco

Large Arctic cisco were also present throughout the study area when sampling began on 3 July (Figs. 21A and B). CPUE fluctuated considerably during the summer, but peak levels were not strikingly different on the two sides of West Dock. Fish had vacated the entire study area by 26 August. Seasonal catch for small Arctic cisco was again characterized by surges in CPUE at the beginning and end of the season. The year-end surge again reflects a return to overwintering grounds in the Sag River.

Eastward migration. Two distinct size cohorts of large Arctic cisco (320–330- and 280–290-mm modes) were present west of the causeway during July. Average CPUE for large Arctic cisco during 13–31 July (period of major activity and continuous sampling) was not significantly associated (Spearman's Rank Correlation Analysis) with either average temperature or average salinity. As with large least cisco, there was also no consistent pattern between prevailing winds and CPUE, with catches often reaching their highest levels during periods of easterly winds (Fig. 22C).

There was no significant association between average CPUE for small Arctic cisco (Sag River) and temperature,

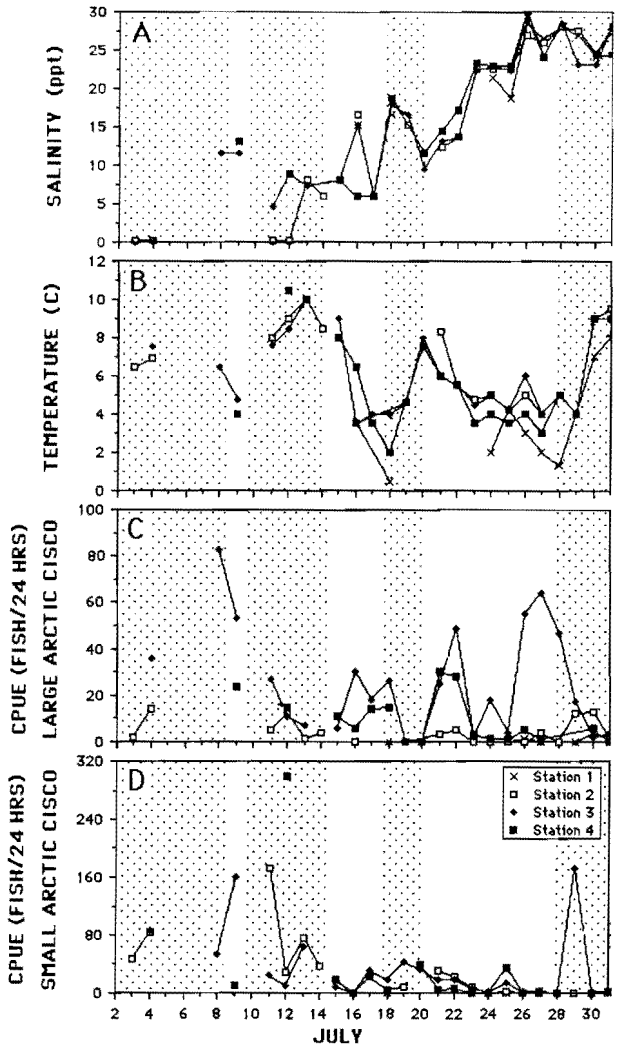

Figure 22. (A) Surface salinity; (B) surface water temperature; CPUE for (C) large (≥250-mm) and (D) small (<250-mm) Arctic cisco at individual fyke nets west of the causeway during 3–31 July 1981. Stippled areas denote periods of westerly winds and clear areas denote periods of easterly winds.

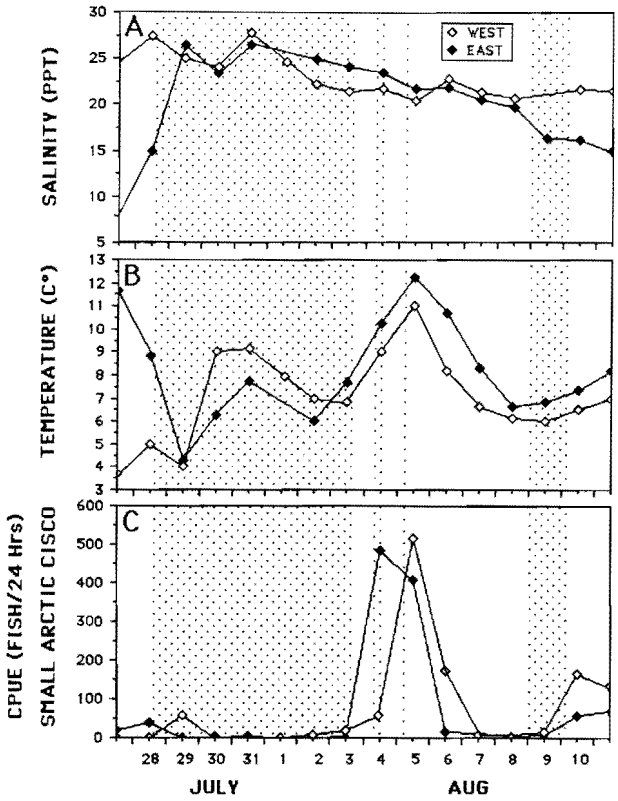

Figure 23. (A) Average surface salinities; (B) average surface water temperatures; (C) CPUE for small (<250-mm) Arctic cisco east and west of the causeway during 27 July–11 August 1981. Stippled areas denote periods of westerly winds and clear areas denote periods of easterly winds.

but there was a significant negative relationship between average CPUE and average salinity ($\rho = -0.686$, $P = 0.001$). Highest catches occurred during periods of westerly winds (Fig. 22D). Small fish may have been responding to fluctuations in salinity and/or the current patterns responsible for those fluctuations.

Movement around West Dock causeway. None of the 987 large Arctic cisco marked west of the causeway were recovered in Prudhoe Bay. A wide coastal distribution, return migrations to the Mackenzie River, and the spatially limited sampling array may have contributed to this result. It was apparent, however, that enough fish were able to bypass West Dock to elicit peak levels in CPUE that were comparable to those observed west of the causeway (Figs. 21A and B). In addition, the two size cohorts observed west of the causeway were also detected in Prudhoe Bay.

An extremely large spike in the CPUE of small Arctic cisco occurred throughout the study area during 3–5 August (Figs. 21C and D). Some have suggested that because this surge occurred immediately following a period of westerly winds, it reflects small Arctic cisco moving into the area from the Colville River. We disagree with this hypothesis.

Winds became mixed early on 3 August. Only then did temperatures on both sides of the causeway begin to rise dramatically, with levels east of West Dock leading levels west of the causeway by 24 hours (Fig. 23B). We speculate that the westward deflection of the Sag plume caused the increase in temperatures. Weak winds on 3–4 July caused the plume to pass around the causeway and down into the lagoon system. Northeasterly winds beginning on 5 July further added to the onshore vector of the plume. Fish passed westward around the causeway and down into the lagoon system with the plume. The large spikes in CPUE were also out of phase by 24 hours and peaks occurred in Prudhoe Bay first (Fig. 23C). This was also the same 2-day period in which least cisco were observed migrating out of Prudhoe Bay.

While we contend that the large midseason surge in CPUE was caused by Sag River Arctic cisco, data do show

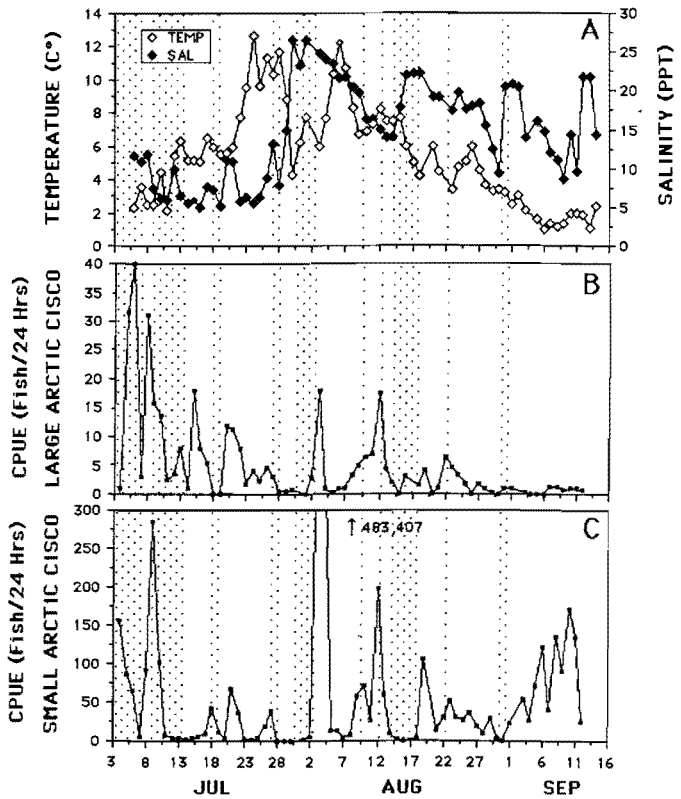

Figure 24. (A) Average surface salinity and average surface water temperature; CPUE for (B) large (≥250-mm) and (C) small (<250-mm) Arctic cisco east of the causeway during 4 July–12 September 1981. Stippled areas denote periods of westerly winds and clear areas denote periods of easterly winds.

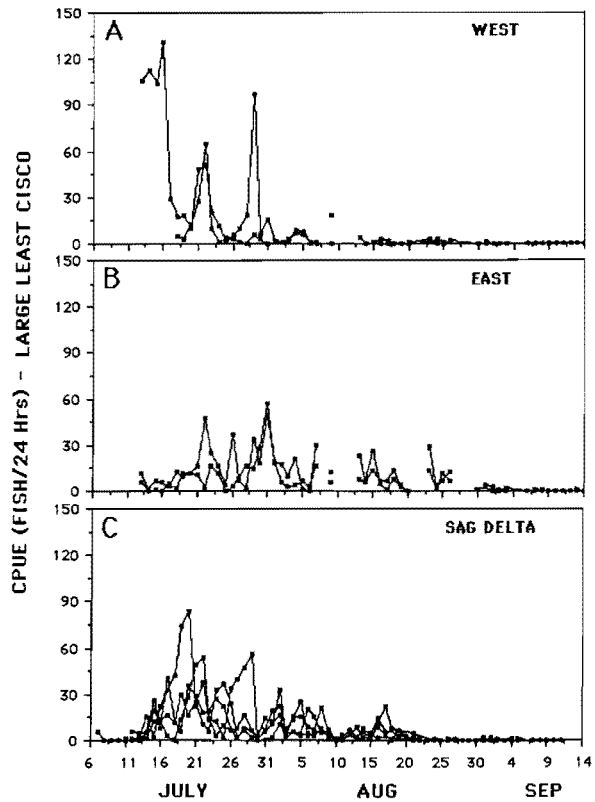

Figure 25. CPUE for large (≥250-mm) least cisco at individual fyke nets located (A) west of the causeway, (B) immediately east of the causeway, and (C) in the Sagavanirktok Delta during 7 July–11 September 1982.

that under certain conditions large numbers of small Arctic cisco move west of the causeway.

East of causeway. There were several indications that both large and small Arctic cisco responded to hydrographic conditions in Prudhoe Bay. CPUE for both groups declined immediately following marine water intrusions on 28–29 July and 13–15 August (Fig. 24). It would again be presumed that fish retreated toward the Sag Delta. Spearman's Rank Correlation Analysis revealed a significant inverse association ($\rho = -0.460$, $P = 0.002$) between average CPUE for large Arctic cisco and average salinity at the Prudhoe Bay stations. A large surge in CPUE for small Arctic cisco occurred on the east side of the causeway in September (Fig. 24C). This occurred during a period of easterly winds and an interim low in salinity (Fig. 24A). Westward deflection of the Sag plume apparently reduced salinity in western Prudhoe Bay and brought entrained fish along with it.

Collectively, data indicate the movement of fish east of West Dock coincides with deflections of the Sag plume and the presence of strong marine fronts.

Westward migration. Large Arctic cisco probably began migrating back to the Colville River in early August. Erratic catch activity was noted on both sides of West Dock during the first 3 weeks of the month. Gill-net data also indicate activity near the causeway during the same period (Fig. 20B). Details of the migration are unclear because of erratic catch levels and the absence of recaptures.

1982

Eight locations were surveyed by fyke net in 1982—four in the immediate vicinity of West Dock and four in front of the Sag Delta (Fig. 2). In addition, there were four trap-net and 34 gill-net sites near West Dock causeway.

Least Cisco

Large least cisco were west of the causeway at the start of sampling on 13 July (Fig. 25A). Catch was nominal in the Sag Delta during the previous 6 days but began increasing on 12 July (Fig. 25C). Sampling may have begun just as the first least cisco were arriving from the Colville River. Large fish vacated waters west of the causeway by the end of July but they continued to be caught east of the causeway until 25 August.

Small least cisco arrived west of the causeway abruptly

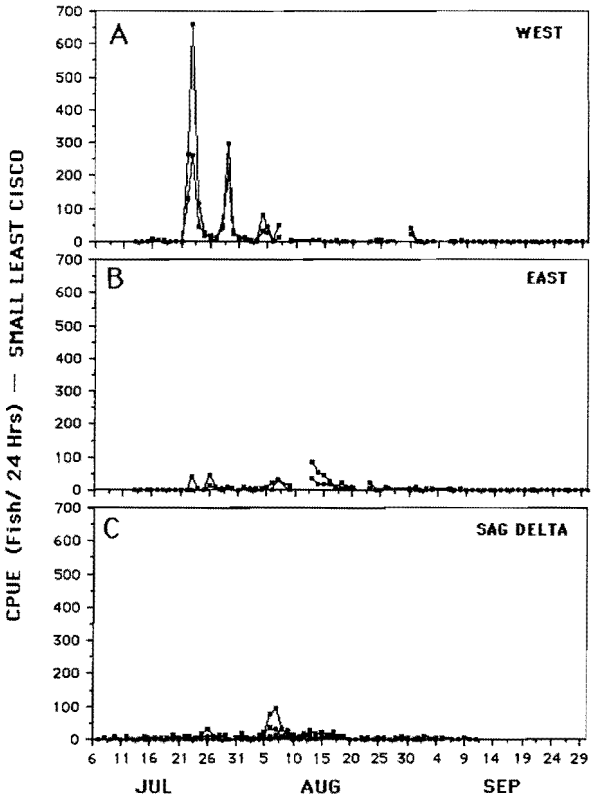

Figure 26. CPUE for small (<250-mm) least cisco at individual fyke nets located (A) west of the causeway, (B) immediately east of the causeway, and (C) in the Sagavanirktok Delta during 7 July–11 September 1982.

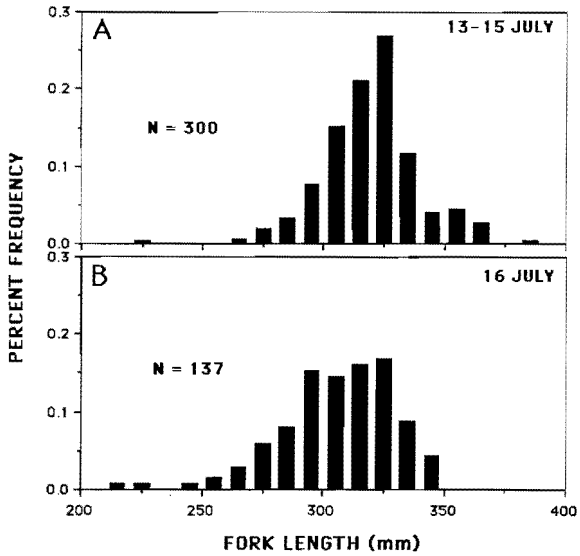

Figure 27. Length–frequency distributions for large (≥250-mm) least cisco collected west of the causeway during (A) 13–15 July and (B) 16 July 1982.

on 22 July (Fig. 26A). Peak catches east of West Dock were comparatively low throughout the season (Figs. 26B and C), suggesting that many fish did not move east of the causeway.

Eastward migration. Fish collected at Station W4 during the first 4 sampling days consisted of several size groups. From 13 to 15 July, the length–frequency distribution was unimodal at 320–330 mm, although skewed to the left (Fig. 27A). On 16 July, the mode flattened and stretched from about 290 to 330 mm (Fig. 27B). The change in shape, which was accompanied by about a 20 percent increase in CPUE (Fig. 25A), was probably due to the appearance of a smaller size group.

Additional surges in the CPUE of both large and small fish occurred on about 21–23 July and 29 July (Figs. 28C and D). The catch on 28 July marked the last major peak in CPUE for large least cisco west of the causeway. There was a small peak in CPUE for small fish on 4 August.

Peaks in CPUE on 21–23 July and 29 July were accompanied by interim peaks in temperature and lows in salinity (Fig. 28). Events occurred at the end of periods dominated by westerly winds. Spearman's Rank Correlation Analysis revealed a significant inverse association ($\rho = -0.536$, $P = 0.018$) between average CPUE for large fish and average salinity for the period 3–31 July (period of catch activity). There was no significant association between CPUE and temperature. This result was undoubtedly affected by high catches during the first 4 days of fyke-netting. Ice was still prevalent in the lagoons and kept temperatures depressed. CPUE for small least cisco was not significantly associated with salinity or temperature.

The lack of significant association between hydrographic parameters and CPUE for small fish was surprising given the trends depicted in Figure 28. We believe that the lack of a statistically significant correlation is an artifact of synoptic sampling techniques.

CPUE increased sharply from 22 to 23 July, apparently in the face of easterly winds and a marine water intrusion (Fig. 28). A closer look indicates that this was not the case. On 22 July, when CPUE first rose to >100 fish/net/day, temperature west of the causeway had reached 13°C. On that day, nets were checked between 0900 and 1200 hours. Easterly winds actually began at 0700 hours on 23 July. Fish were probably not confronted with the marine intrusion until late in the morning of 23 July. When nets were checked between 0930 and 1200 hours on 23 July, results reflected a catch that occurred over the previous 24 hours and a shift in local hydrography that probably occurred over the previous 2–6 hours. Rapid changes in temperature and salinity are not uncommon (Savoie and Wilson 1986). Had the daily temperature–time series been shifted by 1 day, the analysis comparing CPUE for small fish and temperature would have indicated significance at the $P = 0.013$ level.

The association between local hydrography and CPUE depicted in Figure 28 (21–23 and 29 July) is consistent with events observed in 1981 and 1984. Westerly winds resulted in an easterly flow of warm, low-salinity water within the barrier island lagoons. Fish moving in con-

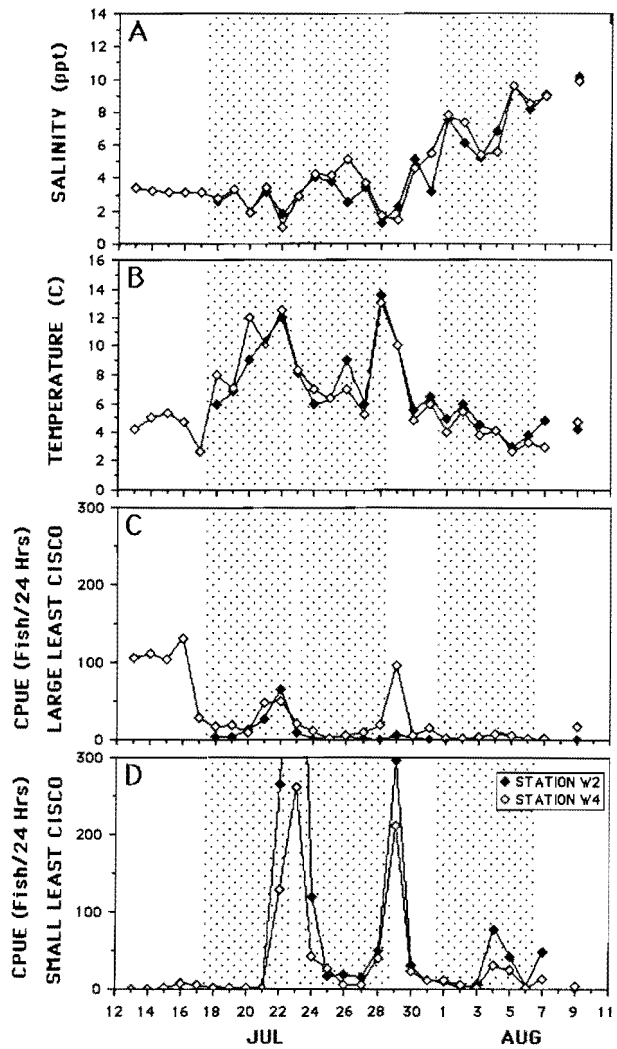

Figure 28. (A) Surface salinities; (B) surface water temperatures; CPUE for (C) large (≥250-mm) and (D) small (<250-mm) least cisco at individual fyke nets west of the causeway during 13 July–9 August 1982. Stippled areas denote periods of westerly winds and clear areas denote periods of easterly winds.

junction with the plume caused CPUE to increase west of the causeway. Just as fish were arriving, winds reversed direction. The ensuing easterly winds resulted in marine water intrusion severe enough to elicit a 6–8°C drop in temperature within 48 hours. With the intrusions and easterly currents came a drop in CPUE as fish retreated westward.

The final surge in CPUE for small fish occurred on 4–5 July (Fig. 28D). A distinctive feature of this catch was that it contained a number of least cisco <140 mm in length. On 5–7 July there was a slight increase in CPUE in the Sag Delta (Fig. 26C), including the first major influx of fish <140 mm. Delta CPUE for fish <140 mm was 0.39 fish/day prior to 5 August and 6.47 fish/day afterwards. CPUE also increased immediately east of the causeway on 6 July with much of the catch consisting of <140-mm fish. Data suggest that fish approaching West Dock on 4–5 July moved past the causeway. Continuous west winds may have enabled them to do so.

Movement around West Dock causeway. For large fish tagged west and recaptured east of the causeway, the most successful recapture rates were associated with fish marked on 13–15 July. Of 299 tagged fish, six (2.00%) were recovered in the Sag Delta and one (0.34%) immediately east of West Dock. Of 780 fish marked after 15 July, one (0.13%) was recaptured east of West Dock. Many of the large fish that passed east of West Dock apparently did so during 13–15 July.

Few small least cisco moved east of the causeway. At no time during the entire season did catch east of the causeway ever approach levels recorded west of the causeway in July (Fig. 26). In addition, only nine (0.33%) of the 2,752 small fish marked west of the causeway were recaptured to the east. This occurred despite a series of nets stretching from West Dock to the eastern Sag Delta.

The absence of small fish east of the causeway is not surprising given that the two biggest buildups of small fish west of West Dock encountered dramatic wind reversals and marine intrusions just as they were arriving in the area. The smaller surge on 4–5 August did not encounter an immediate wind reversal and these fish began appearing in the Sag Delta and immediately east of West Dock several days later.

East of causeway. Some of the large least cisco that passed east of West Dock early in the season may have moved across Prudhoe Bay. On 16 July, CPUE west of the causeway declined from seasonally high levels (Fig. 25A). CPUE in the Sag Delta increased constantly from 12 to 22 July (Fig. 25C). Catch immediately east of West Dock rose only slightly (Fig. 25B). Data suggest that many fish moved directly from the lagoon to the Sag Delta. In addition, of seven lagoon fish recovered east of the causeway, six were taken in the delta.

Large least cisco appeared to move between the Sag Delta and western Prudhoe Bay in conjunction with wind events. From 17 July to 21 August, delta catches were highest during periods of westerly winds and lowest during intervening periods of easterly winds (Fig. 29B). Except for 22–23 July, CPUE in western Prudhoe Bay fluctuated in the exact opposite fashion—low CPUE during westerly winds, high CPUE or influxes of tagged fish from the delta during easterly winds. Results suggest that shifts in the distribution of fish near the Sag Delta tracked the deflection of the plume.

The magnitude of delta CPUE was generally lower during successive periods of westerly winds (Fig. 29). This likely reflects a gradual exodus of fish back to the Colville River. Nominal CPUE in the delta after 20 July indicates that most fish had finally vacated the region by this time.

Temperature and salinity were highly erratic, particularly in front of the delta. We detected no clear association between hydrography and wind events or between hydrography and the distribution of large least cisco. There

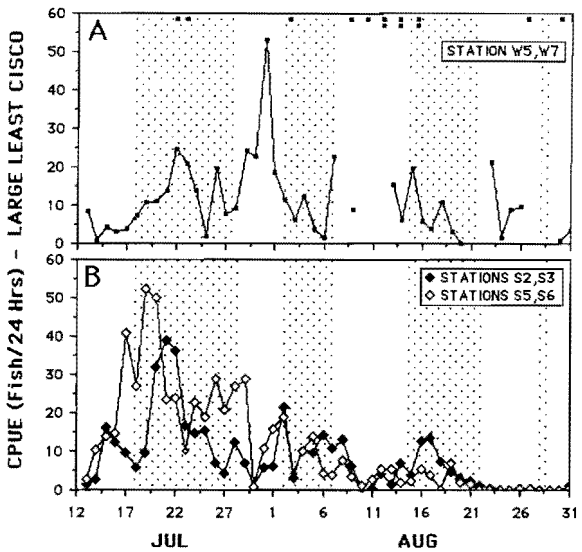

Figure 29. CPUE for large (≥250-mm) least cisco at fyke nets (A) immediately east of the causeway and (B) in front of the Sagavanirktok Delta during 13 July–31 August. Dots along the top of frame A denote fish tagged in front of the Sagavanirktok Delta and recaptured in the vicinity of West Dock causeway. Stippled areas denote periods of westerly winds and clear areas denote periods of easterly winds.

was general decrease in temperature and increase in salinity throughout the season, which is consistent with coastal processes.

Seasonal catch levels for small least cisco east of the causeway were low and prevented analysis of movement.

Westward migration. Gill-net surveys conducted in the vicinity of West Dock depict events late in the season. On 11 August (fyke nets were not operational), large least cisco were taken east of the causeway and at its tip (Fig. 30C). A small catch was observed on the seaward shore of Stump Island. Few fish were caught immediately west of the causeway and inside Stump Island.

The highest catches occurred in the warm, brackish waters of the Sag plume (Figs. 30B and C). Easterly winds were deflecting the plume into the causeway and then westward around its tip. Waters were colder and more saline immediately east of West Dock due to the upwelling of marine water. Results suggest that some fish were moving around the causeway on the return trip to the Colville River in conjunction with the Sag plume.

Only 30 small fish were taken during the 11 August gill-net survey, and most of those were taken east of the causeway.

A second gill-net survey was conducted on 22 August, just prior to the disappearance of large least cisco from

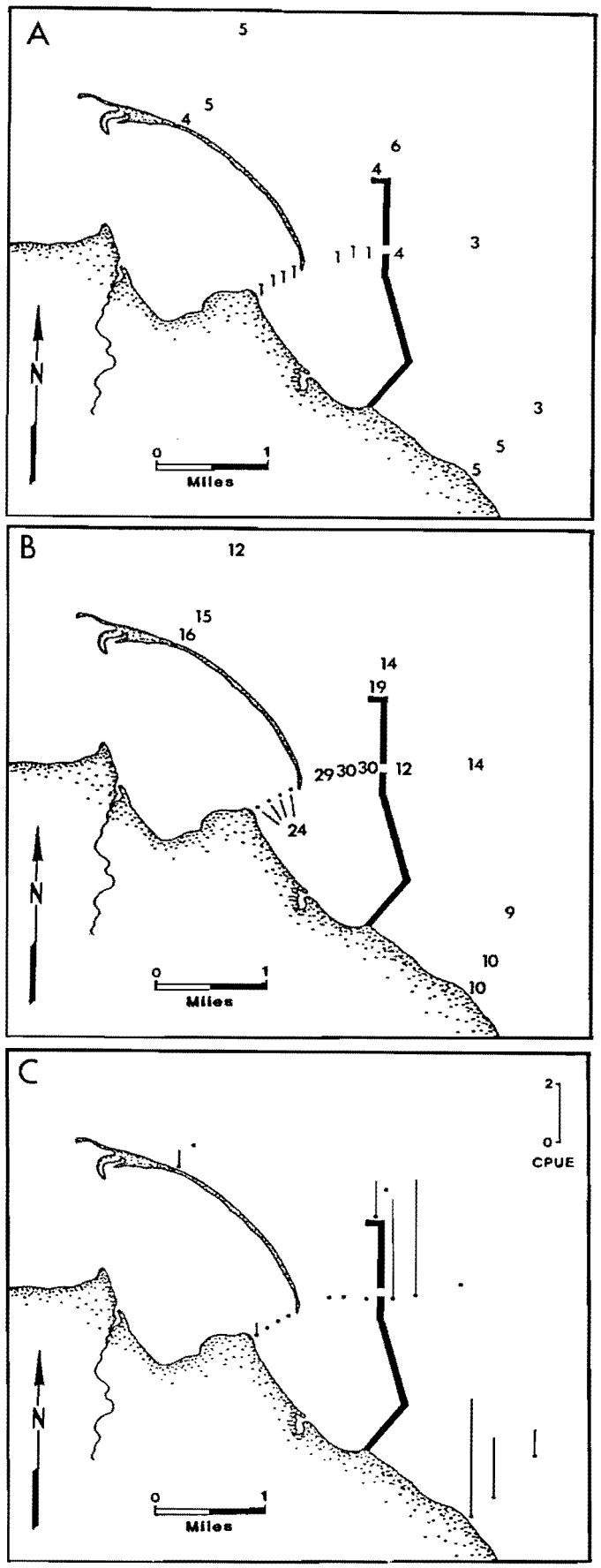

Figure 30. (A) Surface water temperatures; (B) surface salinities; (C) CPUE (fish/hour) for large (≥250-mm) least cisco during the gill-net survey of 11 August 1982. Total effort/station consisted of two replicates of 3–5 hours duration.

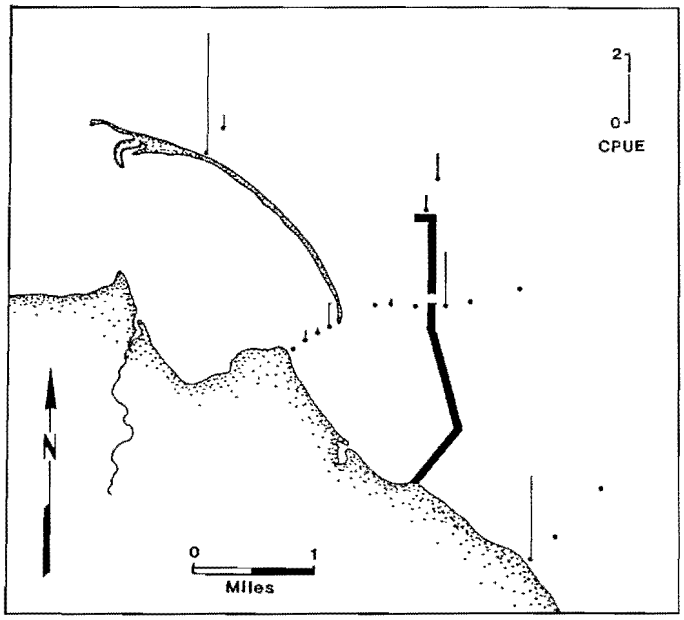

Figure 31. CPUE (fish/hour) for large (≥250-mm) least cisco during gill-net survey of 22 August 1982. Total effort/station consisted of one replicate of 4–7 hours duration.

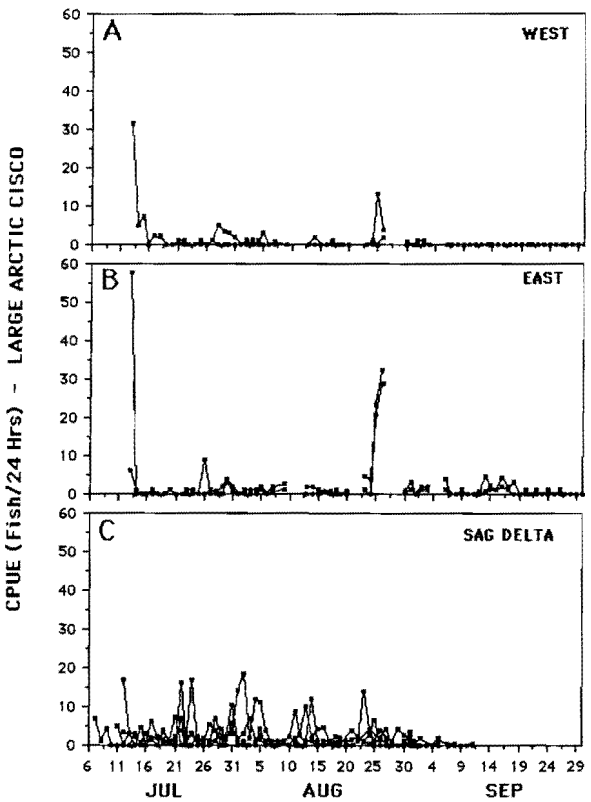

Figure 32. CPUE for large (≥250-mm) Arctic cisco at individual fyke nets (A) west of the causeway, (B) immediately east of the causeway, and (C) in front of the Sagavanirktok Delta during 7–30 September 1982.

the entire study area. The distribution in catch suggests that fish were moving westward around the tip of West Dock and continuing along the barrier islands (Fig. 31). Only 14 small least cisco were caught—seven at the two stations located just seaward of Stump Island. Additional gill-net surveys were conducted on 28–29 August and 4 September, but over 237 hours of effort yielded only 16 fish. Results were consistent with fyke-net data and indicated that most least cisco had already left the Prudhoe Bay area.

Arctic Cisco

Large Arctic cisco were present throughout the study area when sampling commenced (Fig. 32). The largest single-day catches of the season occurred on both sides of West Dock during the first days of operation. The most consistent seasonal activity occurred in front of the Sag Delta and suggests that fish concentrated there. Most fish had apparently left the study area by the end of August.

Small Arctic cisco were far more abundant in front of the Sag Delta throughout the season (note difference in vertical axes; Fig. 33). As in previous studies, surges in CPUE at the end of the summer marked a convergence on the Sag River overwintering area.

Eastward migration. With the exception of two large surges in CPUE on 13 July and 25 August, only 70 large Arctic cisco were taken west of the causeway. The intermittent catch pattern was nondescript and provided no information on movement. The apparent disappearance of large fish after 13 July did not fit with previously described scenarios in which the permanent disappearance of fish west of the causeway occurs in conjunction with the season's first major marine intrusion. From 13 to 15 July salinity held constant and although temperature was low, it actually rose 1°C (Figs. 28A and B). The disappearance of large least cisco may have resulted from fish moving back to the Colville River or eastward past West Dock causeway.

We found no consistent relationship between CPUE for small Arctic cisco and local hydrography or with wind patterns.

Movement around West Dock causeway. There was no clear disparity in peak levels of CPUE for large Arctic cisco on either side of the causeway (Fig. 32). The highest single-day catch actually occurred east of West Dock. None of the 112 fish marked west of the causeway were recovered east of the causeway, which is not unusual for large Arctic cisco (see previous discussions). We found no evidence that large Arctic cisco were prevented from moving east of West Dock causeway.

Although small Arctic cisco were consistently more abundant in front of the Sag Delta, CPUE levels indicated that some fish did move west of the causeway (Fig. 33A). One of the largest spikes in catch occurred late in the season on 25–26 August. This surge probably represents

fish returning to the Sag Delta from the west since it preceded peaks in CPUE east of West Dock (Figs. 33B and C).

East of causeway. Excluding the sharp spikes in CPUE on 13 July and 25 August, most of the seasonal catch for large Arctic cisco was associated with delta stations (Fig. 32). This suggests some concentration in that area. We found no association linking fluctuations in CPUE to either wind patterns or local hydrography.

Small Arctic cisco were most abundant in the Sag Delta, with nets averaging 157.43 fish/net/day for the 1982 season. In contrast, stations immediately east and west of the causeway averaged 21.55 and 13.24 fish/net/day, respectively. Delta stations generally registered higher water temperatures and lower salinities than areas near West Dock. These conditions may have contributed to the greater abundance of fish in the Sag Delta and suggest that small Arctic cisco show some affinity for the river plume.

Of the 33,542 fish marked in the delta, 546 (1.63%) were recaptured there. Only 53 (0.16%) of these fish were recovered near West Dock—16 to the west, 37 to the east. This also implies a minor westward dispersal across Prudhoe Bay and around the causeway.

Eastward dispersal away from Prudhoe Bay was also evident in sequential surges in CPUE across the delta. From 13 to 21 July, a declining catch in the western delta was accompanied by a tremendous surge in CPUE in the eastern delta. Station 6 alone caught 2,915 small Arctic cisco on 19 July (Fig. 33C). How far east fish may have moved is unknown.

Early and late season catches of small Arctic cisco were highest on the western side of the Sag Delta. Because the west channel of the delta contains the highest percentage of overwintering area (Schmidt et al. 1989), catch rates probably reflect an early summer out-migration from and a late summer return migration to overwintering areas.

Plume-directed movement was not quantitatively evident. Two major features probably contributed to this lack of evidence. A massive early dispersal from and a late season return to the western channel of the Sag Delta would tend to override hydrographically related shifts in distribution. Second, gill-net surveys indicated onshore/offshore movement, a pattern that would go undetected in the nearshore grid of fyke-net stations.

Westward migration. Both the 11 and 22 August gill-net surveys indicated that large Arctic cisco were moving westward around the causeway and along the barrier islands in conjunction with the Sag plume (Figs. 34A and 35A). The 22 August survey showed higher CPUE immediately west of the breach (Fig. 35A). While data may indicate greater use of the breach, it is also possible that fish rounding the causeway may have ventured toward Stump Island lagoon. Waters immediately east of the causeway were not as cold (relative to conditions west and north of the causeway) as they had been during the

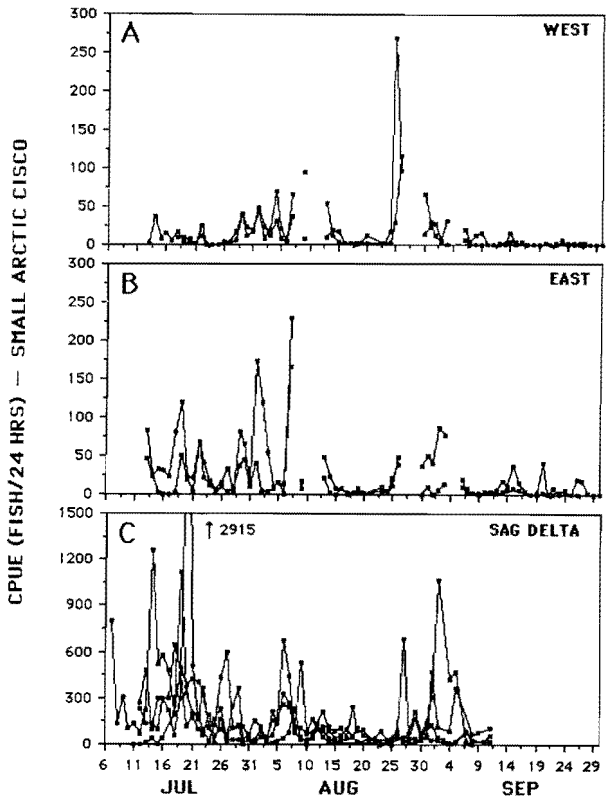

Figure 33. CPUE for small (<250-mm) Arctic cisco at individual fyke nets (A) west of the causeway, (B) immediately east of the causeway, and (C) in front of the Sagavanirktok Delta during 7–30 September 1982.

11 August survey. A complete salinity profile was not available for the 22 August survey.

The pattern in gill-net catches of small Arctic cisco was similar to that for large fish (Figs. 34B and 35B). Whether data depict a return migration of Colville River fish that may have moved into the study area sometime during the season or merely activities at the edge of the Sag River concentration is unknown.

1983

The 1983 study employed a variety of gear types, including beach seines, lampera seines, gill nets, and fyke nets. Fyke nets were used at 10 locations in Prudhoe Bay and at three sites west of the causeway (Fig. 2). Gill nets, beach seines, and lampera seines were used to survey four locations near West Dock causeway. Large fish were not tagged in 1983; however, small fish taken by fyke net were freeze-branded.

Seining and gill-netting provided limited catch data. A total of 57 beach seine sets yielded 42 total fish (i.e., both species, all size classes) while 163 lampera seine sets caught 104 fish. Gill-netting also proved ineffective in capturing small fish: 547 hours of effort yielded only 11 least cisco and 11 Arctic cisco.

Compared with previous studies few small least cisco

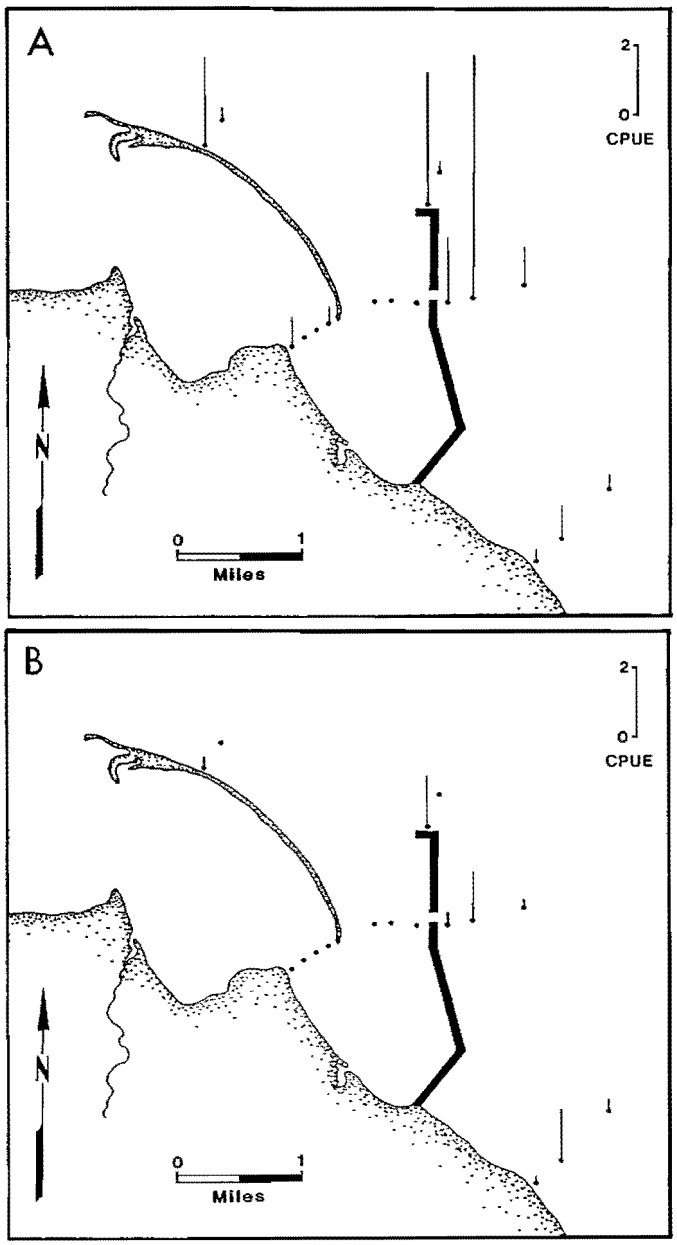

Figure 34. CPUE (fish/hour) for (A) large (≥250-mm) and (B) small (<250-mm) Arctic cisco during gill-net survey of 11 August 1982. Total effort/station consisted of two replicates of 3–5 hours duration.

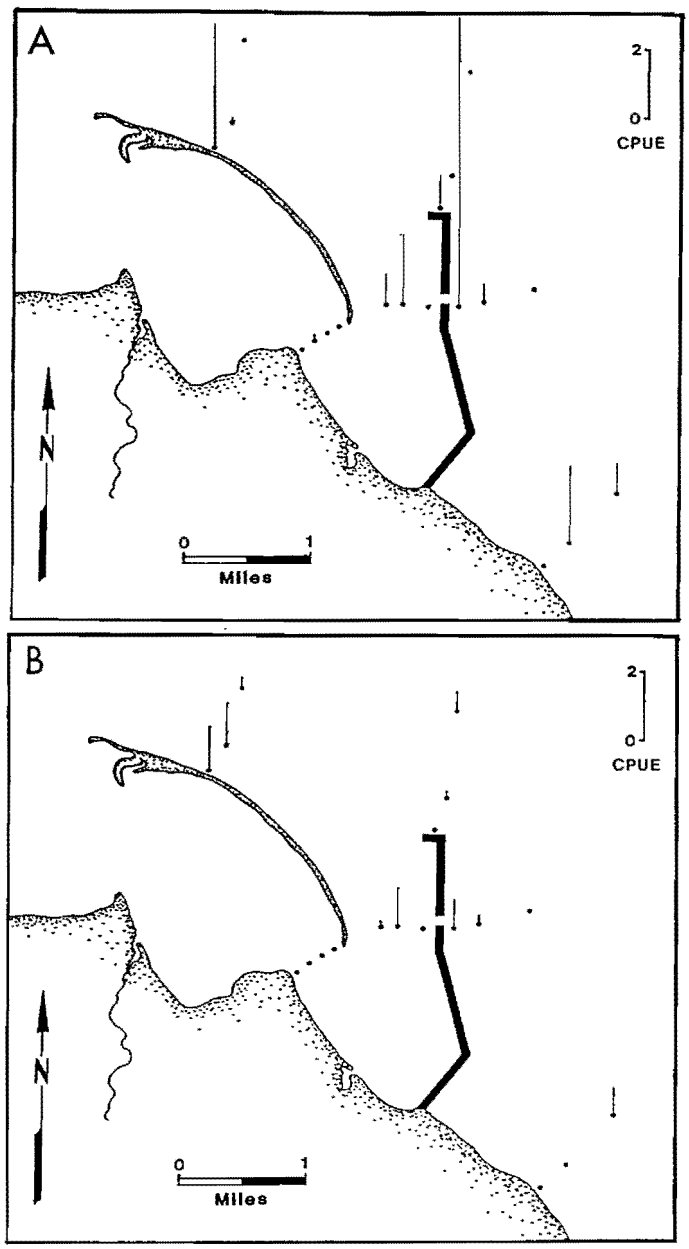

Figure 35. CPUE (fish/hour) for (A) large (≥250-mm) and (B) small (<250-mm) least cisco during intensive gill-net survey of 22 August 1982. Total effort/station consisted of one replicate of 4–7 hours duration.

and large Arctic cisco were taken by fyke net during 1983. Over 623 net-days of effort caught 552 large Arctic cisco (0.87 fish/net/day). There were only 14 instances in which a fyke net caught more than 10 fish/day. In Prudhoe Bay, 516 net days of effort yielded 520 small least cisco (1.01 fish/net/day). The largest single-day catch was 18 fish, and there were only five occasions in which CPUE exceeded 10 fish/day. Over 107 days of effort west of the causeway yielded 341 small least cisco; however, 65 percent (221) of these were taken during one 4-day period. Only three of 128 small least cisco marked during the season were recaptured. Collectively, data were insufficient for assessing movement patterns.

The absence of small least cisco and large Arctic cisco is itself evidence of the mechanisms controlling alongshore movement. The 1983 season was unique in that easterly winds prevailed during the entire first half of the summer. Easterly winds prevented warm discharge water and entrained fish from moving eastward through the barrier island lagoon system. This seems particularly feasible for small least cisco since they were very abundant at the western end of the barrier island lagoon system

during the same year. Four fyke nets located at Oliktok Point (Fig. 1) collectively averaged 89.12 fish/day during 9 July–2 September 1983 (Moulton and Fawcett 1983). The authors also reported peak catches of >1,500 fish/day. By comparison, fyke nets in the Prudhoe Bay area averaged 3.19 and 1.01 fish/day for stations located west and east of the causeway, respectively. The largest single-day catch was only 18 fish.

For large least cisco and small Arctic cisco, analysis of movement patterns was confounded by anomalous meteorological and hydrographic conditions. In 1983, there was a virtual lack of westerly winds from 22 June to 1 August. In addition, the ice pack remained close to shore throughout most of the summer. Floe ice regularly occupied offshore waters and occasionally entered Prudhoe Bay. Icemelt contributed substantial volumes of fresh, cold water to the surface offshore water mass. These ice conditions appeared to have a considerable effect upon nearshore hydrography (Woodward-Clyde Consultants 1983).

The net effect of conditions in 1983 was to elicit fluctuations in temperature and salinity that did not conform to the standard mechanisms governing nearshore hydrography. Large temperature fluctuations occurred in Prudhoe Bay because of changes in wind velocity and only slight changes in wind direction. Conditions were subject to the influence of the ever-present ice. The anomalous hydrographic conditions plus the complete absence of tagging data precluded detailed interpretation of fish movements.

There were general features worth noting. The overall pattern in large least cisco catch was similar to those in other years. Fish appeared to vacate waters west of the causeway by the end of July in conjunction with the season's first major marine intrusion (Fig. 36A). Fish that moved into Prudhoe Bay remained active until the end of August (Fig. 36B). Small Arctic cisco were most abundant in Prudhoe Bay, with much lower catches occurring west of the causeway (Figs. 36C and D). As in other years, catch was highest very early (out-migration) and very late (return migration) in the season.

RESIDENCY TIME OF COLVILLE RIVER FISH

A consistent trend in all 4 study years was that Colville River fish vacated waters west of the causeway before they disappeared from waters east of the causeway (Figs. 4, 11, 17, 21, 25, 32, and 36). Most of the midseason catch west of the causeway was associated with fish from Prudhoe Bay migrating through the area on their return trip to the Colville River. In all years, this difference arose in conjunction with the first major marine intrusion of the year, which typically occurs in late July/early August. This midseason intrusion permanently alters coastal hydrography by making conditions more marine. It is also partially responsible for the difference in residency time.

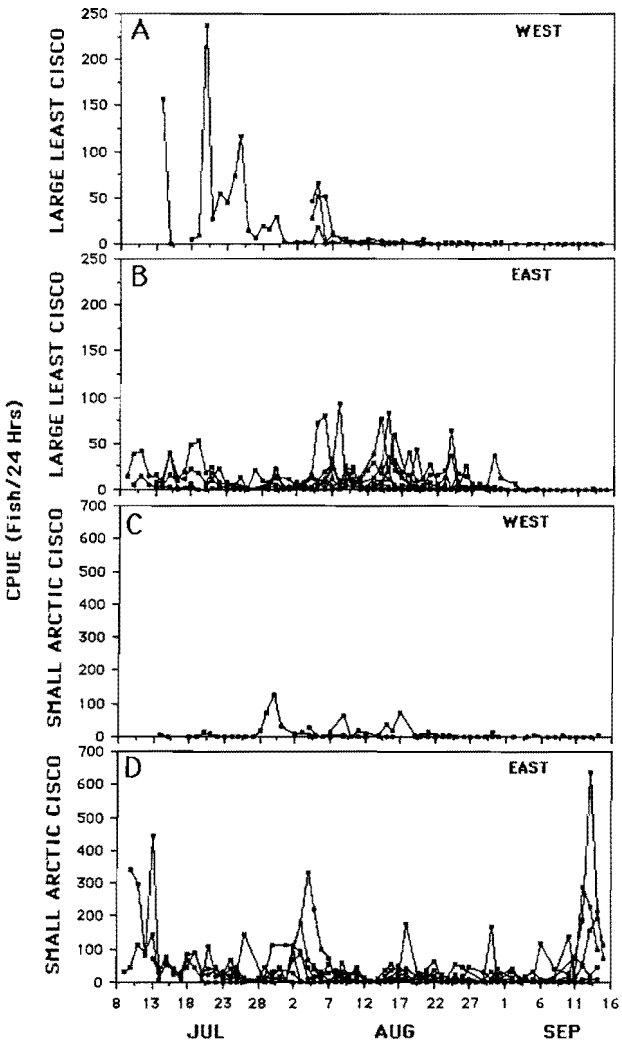

Figure 36. CPUE for large (≥250-mm) least cisco at individual fyke nets located (A) west and (B) east of the causeway, and for small (<250-mm) Arctic cisco at individual fyke nets located (C) west and (D) east of the causeway during 9 July–15 September 1983.

East winds cause marine water to enter the eastern end of the barrier island lagoon system, which in turn causes fish to retreat westward. Because of the permanence of the effect and the lateness of the season, fish do not return to the study area. On the ensuing shift to westerly winds, marine water that accumulates around the causeway is pushed into Prudhoe Bay from the northwest. This marine front causes fish in Prudhoe Bay to retreat eastward to the Sag Delta. Renewed occupancy of Prudhoe Bay and/or a westward migration to the Colville River occurs only after the marine front dissipates. The same intrusion effectively splits the populations and is partially responsible for the difference in residency times.

COMMERCIAL TAG RETURN RATES

Helmerick's commercial gill-net fishery, located in the lower Colville River delta, is in operation from October

to December of each year and is a valuable source of tagged least and Arctic cisco. Tags were analyzed to determine if commercial recapture rates differed based upon the side of the causeway on which fish were marked. Data were adjusted to compensate for the size selectivity of commercial gill nets (Appendix A).

With the exception of least cisco in 1981, there were no significant differences in tag recapture rates at Helmerick's fishery for either least or Arctic cisco based upon the side of the causeway on which fish were released (χ^2 analysis, $P = 0.356$–0.973).

Although the difference in return rates was not significantly different for least cisco in 1981 ($\chi^2 = 3.69$, $P = 0.055$), it was close enough to merit discussion.

As previously discussed, two distinct size cohorts of large least cisco were detected moving into waters west of the causeway in 1984. The larger size-class (Group 1: 250–400 mm, mode = 310–320 mm) appeared on 4 July, the smaller size-class (Group 2: 250–390 mm, mode = 290–300 mm) on 18 July. Analysis of commercial tags revealed no significant difference ($\chi^2 = 0.419$, $P = 0.518$) between fish tagged east and west of the causeway prior to 18 July (Group 1 only). There was also no significant difference ($\chi^2 = 0.977$, $P = 0.323$) between fish marked after 18 July (Groups 1 and 2 combined). However, the overall return rate for Group 1 (all fish prior to 18 July) was significantly higher ($\chi^2 = 32.000$, $P < 0.001$) than the overall return rate for the combined groups (all fish after 18 July).

The difference in return rates was not due to the causeway and was not due to size differential (data were corrected to account for the size selectivity of commercial nets). The two groups inherently acted differently, perhaps in the timing or pathway of their year-end migration to the Colville River.

The relevance to 1981 is that multiple size cohorts with inherently different migration patterns could bias commercial tag return analysis. In 1981, several size groups were in the area when sampling began and there was no way to distinguish any group-specific difference in susceptibility to commercial nets. Return rates in 1981 thus represent a composite of cohorts. Lower return rates for least cisco tagged east of the causeway (nearly significant: $P = 0.055$) may merely reflect a disproportionate distribution of different size groups on opposite sides of West Dock causeway.

EFFECTIVENESS OF CAUSEWAY BREACH

Although the causeway breach was installed specifically as a fish passageway, the Prudhoe Bay summer studies have led to a common consensus by principal investigators that fish do not use the breach to any great extent (T. Cannon, K. Critchlow, B. Gallaway, and L. Moulton, pers. comms.). We agree with this consensus.

SUMMARY

Arctic anadromous fish overwinter in or near major freshwater drainages of Alaska's North Slope. During the brief ice-free summer season, fish disperse into coastal waters to feed. Near the end of summer and prior to freeze-up, fish return to overwintering grounds where they presumably spend the long arctic winter in deepwater holes and channels.

Least cisco in the central Beaufort Sea spawn and overwinter in the Colville River and do not use the Sag River for either purpose. Arctic cisco spawn in the Mackenzie River in Canada are are transported into Alaskan waters by alongshore currents. They take up residency in Alaskan rivers until they approach sexual maturity, at which point they return to the Mackenzie River to spawn. Once these transients take up temporary residency in Alaskan rivers they are believed to maintain some degree of fidelity.

During the 1981–1984 studies, most of the large Arctic cisco found in the study area originated from overwinter areas in the Colville River. Conversely, most of the small Arctic cisco originated from Sag River overwintering areas. The reasons for this segregation are unclear but may relate to differential recruitment and/or the quality of overwintering habitats.

Colville River Fish (Least Cisco, Large Arctic Cisco)

The extent of eastward dispersal from the Colville River depends upon prevailing wind patterns. Westerly winds cause warm, low-salinity water of the Colville River to flow eastward through the barrier island lagoons. Fish travel in conjunction with this plume. Easterly winds inhibit the eastward flow of the plume, which in turn curtails eastward dispersal of fish. For any given season, net eastward dispersal is a function of wind periodicity. The greater the percentage of westerly winds the farther the eastward migration, and vice versa.

Eastward dispersal is also a function of size. Progressively smaller size classes arrive at West Dock on progressively later dates. This trend reflects size-dependent swimming speed. Larger, more powerful fish can traverse coastal distances more rapidly. The segregation of size classes and wind periodicity are thus the two major factors determining the extent of eastward dispersal through the barrier island system. In years dominated by easterly winds many of the smaller size classes may never even reach West Dock causeway (e.g., small least cisco in 1983).

If Colville River fish do reach West Dock, further eastward dispersal can be blocked by the structure itself. During westerly winds, the warm water plume and the fish traveling with it move around the tip of West Dock and continue eastward. During easterly winds, the causeway causes strong marine intrusions to penetrate the eastern end of the barrier island lagoon system. Fish that have

not already passed east of the causeway retreat westward from the intrusion. A return to westerly winds purges the marine water from the system and fish may again approach the causeway and move around it. Alternating winds cause the system to oscillate and may allow fish to approach the causeway several times during a season.

The causeway can also block eastward movement by diverting fish toward more marine waters. If this diversion causes fish to encounter strong marine fronts they may again retreat westward (e.g., large least cisco in 1984).

Although fish pass east of the causeway during westerly winds there are sometimes temporary buildups of fish along the causeway's western face. By itself this delay is not critical; however, it does mean that fish remain in an area that is hard-hit during ensuing marine intrusions. Such a delay and an ensuing wind shift blocked a large group of small least cisco from passing east of West Dock in 1982.

Fish dispersing westward from the Colville River have only a limited time frame in which to pass east of West Dock. In accordance with natural physical processes, an intense marine intrusion in late July/early August permanently changes nearshore hydrography. Once this event occurs, marine conditions in the eastern end of the barrier island lagoon system cause fish to retreat westward. They do not appear in the causeway/Prudhoe Bay area for the remainder of the season.

Thus, in order for Colville River fish to disperse east of West Dock they must encounter a high enough proportion of westerly winds such that they reach the causeway, and they must be lucky enough not to encounter marine intrusions once they get there. All this must occur before the end of July, prior to the first major marine intrusion of the year.

Fish that do pass east of West Dock appear to alter their distribution in response to changes in local hydrography. Easterly winds deflect warm, low-salinity water from the Sag River to the west and fish may become more abundant in Prudhoe Bay. Westerly winds can cause marine intrusions to enter Prudhoe Bay from the northeast and, in conjunction with the eastward deflection of the Sag plume, cause fish to retreat toward the haven of the Sag Delta. There may also be some onshore/offshore movement relative to the configuration of the Sag plume.

Fish begin trickling back to the Colville River as soon as they pass east of the causeway. It may take anywhere from 2 to 4 weeks for them to completely vacate waters east of West Dock. The exodus from Prudhoe Bay often occurs in pulses, at times in conjunction with the westward deflection of the Sag plume around the tip of West Dock. It is unclear how strongly fish depend upon the Sag plume to provide a warm-water pathway around West Dock. Regardless of wind periodicity and deflection of the Sag plume, Colville River fish are gone from the Prudhoe Bay area by the end of August.

Some large Arctic cisco that pass east of West Dock apparently continue migrating toward spawning grounds in the Mackenzie River system. Seventeen Arctic cisco tagged in the Prudhoe Bay/Simpson Lagoon area have been recaptured far to the east of the Prudhoe Bay region: two at Griffin Point (Craig and Haldorson 1981; Nelson et al. 1987; Cannon et al. 1987b), six at Barter Island/Kaktovik (Griffiths and Gallaway 1982; Nelson et al. 1987; Cannon et al. 1987b), one at the Mackenzie River delta (Gallaway et al. 1983), and eight in Mackenzie Bay (W. Bond, pers. comm.). One of the fish recovered at Kaktovik traversed the 170-km distance in 7 days (Nelson et al. 1987).

The midseason marine intrusion coupled with the presence of West Dock is partially responsible for longer residency times east of the causeway. Easterly winds and the marine intrusion west of the causeway cause fish to retreat back to the Colville River. The ensuing shift to westerly winds pushes this marine water into Prudhoe Bay and causes fish to retreat toward the Sag River. Renewed occupancy of Prudhoe Bay and a return migration to the Colville River occur only after the marine front has dissipated. The same intrusion effectively splits the population and causes differential residency times.

Tag return data from the Colville River commercial fishery indicate that large least and Arctic cisco return to overwintering areas regardless of whether they do or do not pass east of West Dock. This is consistent with CPUEs in the study area that indicate that Colville River fish leave the Prudhoe Bay area long before freeze-up.

Sag River Fish (Small Arctic Cisco)

The movements of small Arctic cisco also appear to be modified by hydrographic conditions. This conclusion has been offered by numerous investigators—Griffiths and Gallaway (1982), Griffiths et al. (1983), Woodward-Clyde Consultants (1983), Biosonics, Inc. (1984), Critchlow (1983), Moulton et al. (1986), and Cannon et al. (1987a). Detailed examples, however, are far less numerous than for Colville River fish for several reasons.

First, seasonal catch patterns in Prudhoe Bay and in front of the Sag Delta are typically characterized by large surges early and late in the season. These surges represent dispersal from and a return to overwintering areas in the west channel of the delta. This migratory pattern tends to override hydrographically related shifts in distribution.

Second, small Arctic cisco are most abundant in front of the Sag Delta and appear to modify their distribution in response to the trajectory of the Sag plume. Plume configuration can shift distributions such that fish are beyond the range of sampling grids. Fish may move east of Prudhoe Bay or even move offshore. Onshore/offshore movement coupled with east–west movement is one reason why responses of Colville fish to physical processes were far less evident east of the causeway than to its west. The barrier island lagoon system acts more like a one-dimensional system with only an east–west component.

For small Arctic cisco, dispersal west of West Dock causeway occurs during westward deflection of the Sag plume (easterly winds). An extremely strong pulse of fish moved around the causeway in 1981 under such conditions. Easterly winds during the first half of 1983 caused Sag River fish to move as far west as Oliktok Point. However, the net effect of West Dock on the westward dispersal of small Arctic cisco is less clear than it is for the eastward dispersal of Colville River fish. Lower CPUE west of the causeway may merely reflect greater distances away from the area of high concentration in front of the Sag Delta. In 1984, abundance levels from the delta to West Dock petered out before reaching the causeway.

Unlike Colville fish approaching the causeway from the east through the barrier island lagoons, plume-directed movement westward around the causeway may take Sag River fish offshore and beyond the range of sampling gear in Prudhoe Bay. Since offshore movement occurs naturally in front of the Sag Delta (Griffiths et al. 1983), a similar component to westward dispersal may also occur with or without the causeway. This further obscures West Dock's effect on alongshore dispersal.

DISCUSSION

During easterly winds, West Dock causeway blocks the eastward dispersal of fish from the Colville River by modifying nearshore hydrographic conditions. While the actual amount of habitat directly affected is small, it does render nearshore areas east of the causeway inaccessible to some portion of the population. B. J. Gallaway (pers. comm.) speculates that 40 percent of the viable warm-water, nearshore habitat in the central Beaufort Sea lies east of West Dock causeway.

West Dock's effect on dispersal of Arctic cisco from the Sag River is less evident. Theoretically 60 percent of the viable warm-water habitat lies west of the causeway, but any failure of fish to exploit this area may depend more on their tendency to concentrate near the Sag Delta.

The net effect of habitat loss is presently under study. There are numerous other factors that must be integrated into the analysis. Loss of habitat is less relevant if only small segments of the population are affected. L. L. Moulton (pers. comm.) calculated that in 1984 only 4 percent of the small least cisco population from the Colville River even reached the causeway. Conversely, he estimated that 50 percent of the large least cisco population migrated into the study area. The net worth of feeding habitat along the coast may vary. Moulton et al. (1986) found that prey densities were significantly higher west of the causeway in 1984. Cannon et al. (1987a,b) found that prey densities were higher east of the causeway in 1985. Because the main reason for coastal dispersal in summer is to forage, food availability is a paramount issue in determining habitat value. Growth rates and population sizes are being assessed to determine if there are any direct impacts to anadromous fish populations from either the Colville or the Sag Rivers.

This paper has addressed just one of many factors that must be considered in assessing the net impact of petroleum operations in Prudhoe Bay on arctic anadromous fish populations. Whether disruption to coastal feeding migrations is truly detrimental to fish populations will depend upon results of feeding, growth, reproductive, and population studies. At stake is resolution to a basic conflict in perspectives: are man-induced intrusions seriously impacting a delicate and fragile environment, or are they merely insignificant quirks to populations that have survived for millions of years?

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APPENDIX A. STATISTICAL METHODS

Three basic types of statistical analyses appear in the body of this paper. They are

1. Pairwise comparisons of mean catch per unit of effort (CPUE) or mean physical measurement (temperature, salinity);
2. Correlation analyses of physical variables with CPUE and among CPUE values;
3. Tests of mark–recapture rates and their adjustment under specific recapture regimes.

The approach taken throughout this paper is to rely on simplified statistical methods (t-test, Spearman's Rho, etc.) with careful validation of the assumptions underlying these tests. An outline follows of the approach taken in the testing of these assumptions. Details of checks on

specific data sets will not be presented here for the sake of brevity.

Pairwise Tests of Means

Most of the comparisons of means (CPUE, temperature, etc.) that appear in the body of this paper were constructed from daily measurements. To apply a simple test (e.g., a *t*-test) of mean levels to daily replicates, several important assumptions must be considered. They are

1. Independence or approximate independence of replicates;
2. Sufficient sample size for application of large sample properties of the test or small sample distribution results such as normality for a *t*-test;
3. For large sample results, independence of the mean and variance.

Because of the nature of the replication (daily measurements) the question of independence of replicates is an important one. For all applications of *t*-tests a check of independence of replicates was performed. This was accomplished using two methods:

1. Estimation of first- and second-order autocorrelation coefficients and their standard errors (see Box and Jenkins 1976);
2. Durbin's test for autocorrelation (see Neter and Wasserman 1974).

In all but several isolated cases no significant autocorrelation of short-term (1–20-day) replication of CPUE or physical variables was observed. When a significant degree of autocorrelation was encountered, tests for changes in mean levels were abandoned.

For the distributional assumptions (2 and 3 above) two cases were considered specifically. In the majority of the applications of the *t*-test, sample sizes were sufficient to apply the normal approximation to the *t*-test (see Neter and Wasserman 1974). The remaining assumption of independence of mean and variance was assessed and dealt with by transformation when necessary. Transformation was most commonly needed with the CPUE data, which occasionally showed marked skewedness. In the cases where sample sizes were sufficiently small to warrant investigation of normality assumptions this was carried out using a Kolmogorov-Smirnov test (see Conover 1971).

Tests of correlation among CPUE and physical variables were performed using a Spearman's Rho nonparametric correlation coefficient (see Conover 1971). This correlation coefficient was used because of the nature of the variables being correlated: that is, the non-normality of the CPUE variables with the additional problem of small sample sizes. It was necessary in many situations to apply small sample distribution results to perform the test (see Conover 1971).

To test for differences in recapture rates, a Chi-square test was used. This test was applied to recapture data using several different methods. In cases where recapture methods were not size-selective (usual fyke-net catches) the standard Chi-square test was applied. A second approach was used when the recapture method was size-selective, for example at Helmericks' fishery. To adjust for selective recapture the method outlined in Ricker (1975:Section 3.7) was applied.

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Recruitment of Arctic Cisco (*Coregonus autumnalis*) into the Colville Delta, Alaska, in 1985

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Abstract. In 1985, westward movement along the Beaufort Sea coast between Kay Point, Yukon Territory, and the Colville River, Alaska, was documented for young-of-the-year Arctic cisco. The observed movement pattern closely paralleled the recruitment pattern previously hypothesized. The westward movement and recruitment into the Colville Delta was facilitated by persistent easterly winds in the early and middle parts of the open-water season. Larger-bodied members of the age group arrived at the deltas of the Colville and Sagavanirktok Rivers first, with smaller fish arriving later. In 1986, recaptures at Kay Point of eight adult Arctic cisco previously tagged near Prudhoe Bay provided further direct evidence of the exchange of this species between Prudhoe Bay and the Mackenzie River region.

INTRODUCTION

Arctic cisco (*Coregonus autumnalis* Pallas) has received considerable attention along the Alaskan Beaufort Sea coast because of its importance in the regional domestic fishery and perceived susceptibility to impacts from industrial development (Moulton et al. 1986; Gallaway et al. 1989). Although Arctic cisco is abundant throughout the Alaskan Beaufort Sea coastal region, often being the most abundant species in studies of coastal fishes, no spawning areas have been documented in the region. The nearest known spawning areas are in the Mackenzie River drainage in Canada (Hatfield et al. 1972). It has been hypothesized that the Arctic cisco in Alaska originate from the Mackenzie River spawning groups (Gallaway et al. 1983).

Information used by Gallaway et al. (1983) to support the Mackenzie-origin hypothesis for Arctic cisco in Alaska included

1. The absence of known Arctic cisco spawning areas, while many spawning areas for other coregonid species in the Beaufort Sea region are documented;
2. The absence of fish in spawning or spent condition;
3. The low tag return rate from Arctic cisco tagged in the region, as compared to returns of tagged least cisco, *C. sardinella* (the indication is that large Arctic cisco leave the area within a year or two of being tagged, whereas least cisco continue to be caught up to 10 years after tagging).

It was established that with water currents generated by typical meteorological patterns (average northeasterly winds at 5 m/sec generating a 15 cm/sec coastal current), age-0 and -1 Arctic cisco could be passively transported into the Colville area in about 35 days or less.

The Mackenzie-origin hypothesis was based strictly on the apparent discrepancies between least cisco and Arctic cisco life history patterns as determined from catch and tag return data available prior to 1982. Since that time, a number of field studies have been conducted (Critchlow 1983; Griffiths et al. 1983; Woodward-Clyde Consultants 1983; Biosonics, Inc. 1984; Moulton and Fawcett 1984; Fawcett et al. 1986; Moulton et al. 1986). All the observed patterns in Arctic cisco life history information have been consistent with the Mackenzie-origin hypothesis.

Three factors that have confounded a true test of the Mackenzie-origin hypothesis, however, are

1. There were 4 years of weak recruitment in the region between 1981 and 1984, although major fish studies were being conducted;
2. There have been virtually no returns of tagged Arctic cisco from Canada, despite the release of over 20,400 tags prior to 1986 (one was recaptured in September 1983);
3. Geographic coverage by studies has been limited, with no significant sampling east of the Sagavanirktok River prior to 1985.

In 1985, geographic coverage of fish movement along the Beaufort Sea coast was expanded, through three independent programs, covering the area between the Babbage River, Canada, and the Colville River (Fig. 1). The objective of this study is to (1) describe the recruitment of age-0 Arctic cisco into the Colville Delta in 1985, and (2) analyze patterns of juvenile Arctic cisco catch to further evaluate the Mackenzie-origin hypothesis.

METHODS

Sampling Gear

Sampling in the Colville Delta was conducted from early July to mid-September 1985 with frame fyke nets

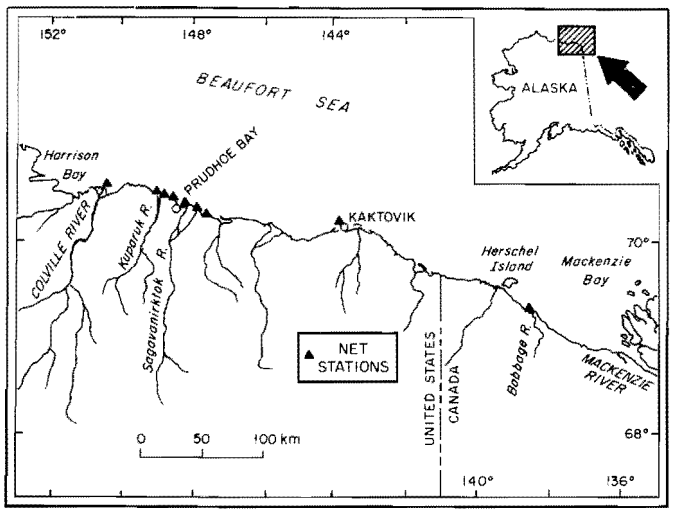

Figure 1. Beaufort Sea coastal region between the Mackenzie and Colville Rivers showing locations of fyke nets in 1985.

consisting of double cod-end traps, two wings, and a lead stretched from shore to the traps at a right angle to the shoreline. Each trap had a stainless steel frame (1.7 m deep, 1.8 m wide) attached to a knotless nylon net bag (3.7 m long, tapered to 0.9 × 0.9 m on a side) of 1.27-cm stretched mesh. Leads and wings were 2.5-cm stretched mesh. Wings were 15 m long and typically 1.5 m deep. Leads were typically 1.5 m deep, varying in length depending on water depth and bottom topography. In some areas of deep water, the depth of the wings and leads was increased to 3.0 m.

Fish Sampling and Tagging

The fyke net traps were emptied daily; fish were placed into floating live pens for processing. Lengths of anadromous species were recorded to the nearest millimeter. Usually all anadromous species were measured, but when large catches of small fish were made, subsamples of 100 were measured and the remainder counted and released. The otoliths from 33 small Arctic cisco (<120 mm) captured after 26 August were used to evaluate the age composition of the smaller cohorts.

Anadromous fish >250 mm were tagged below the dorsal fin with a numbered Floy FD 68 anchor tag and released. Past studies in the region (Griffiths and Gallaway 1982; Critchlow 1983; Griffiths et al. 1983; Moulton et al. 1986) indicate that 250 mm is the minimum size at which ciscoes and whitefish should receive an injection tag.

Information Sources

The catch information used in the analysis was derived from three independent studies:

1. Data from 1985 Canadian catch records were supplied by Mr. William Bond, Fisheries and Oceans, Canada, Freshwater Institute, Winnipeg, Manitoba;
2. Data from Kaktovik to Storkersen Point were obtained from the US Corps of Engineers' 1985 Endicott Environmental Monitoring Program as reported in data appendices in Envirosphere (1986) (methods used in this study were virtually identical to those described above);
3. Information from the Colville River as described above.

RESULTS AND DISCUSSION

1985 Recruitment Pattern

In the 1985 sampling of the Colville River, almost all Arctic cisco were captured in the delta nets (4,172 fish) as opposed to river nets (52 fish). Arctic cisco were virtually absent from the delta until mid-August, at which time medium (150–200-mm) and large (>250-mm) fish began to enter the river mouth. Approximately three-fourths of the 4,172 Arctic cisco captured in the delta were <120 mm. The subpopulation of small Arctic cisco was composed primarily of age-0 fish, i.e., the 1985 year-class. This group of small fish first appeared in the study area on 26 August. The number of small fish increased during the following week (2–6 Sept.) and appeared to be increasing further during the last week of sampling. The largest catch was recorded on 11 September, the final day of sampling.

As the juvenile Arctic cisco moved into the Colville Delta, larger fish reached the delta prior to smaller fish. The length–frequency distribution of small Arctic cisco during the last 3 weeks of sampling revealed a large peak of age-0 fish at 70–74 mm for 26–30 August. The mode decreased to 65–69 mm the following 2 weeks, as the small members of the age group arrived. By otolith readings the size range of age-0 fish was 62–80 mm and for age-1 fish was 82–98 mm. Smaller fish were measured but were not represented in the sample retained for aging. The age-1 group (or 1984 year-class) is weakly represented, showing a mode at 85–90 mm.

Regional Considerations

A westward movement of age-0 Arctic cisco along the Beaufort Sea coast was indicated by the catch of young-of-the-year Arctic cisco at various sampling locations between Kay Point at the mouth of the Babbage River and the Colville River (Table 1). The date of first capture of age-0 Arctic cisco at various sampling locations demonstrates a westward movement of fish from Kay Point (50 miles west of the Mackenzie River) on 13 July to the Colville River delta on 26 August (Fig. 2). The criterion for date of first capture was a catch of two or more age-0 Arctic cisco followed by increasing catches in subsequent

Table 1. Estimated rates of movement for age-0 Arctic cisco between various locations along the Beaufort Sea coast and the Colville Delta.*

Location	Date of initial capture†	Distance to Colville (km)	Days elapsed, location to Colville	Rate of movement (km/day)
Kay Point	13 July	480	44	10.9
Kaktovik	11 Aug.	255	15	17.0
Foggy Island Bay	16 Aug.	105	10	10.5
Eastern Sagavanirktok Delta	20 Aug.	90	6	15.0
Niakuk Island	20 Aug.	80	6	13.3
East base of West Dock	21 Aug.	64	5	12.8
Storkersen Point	23 Aug.	48	3	16.0

* Source: Mr. William Bond, Fisheries and Oceans, Canada, Freshwater Institute, Winnipeg, Manitoba.

† Day of first capture was defined as day when two or more fish were caught followed by increasing catches in subsequent days.

days. At each of the sampling locations peak catches of age-0 fish generally occurred a few days after the date of first capture, with the eastern cod-end of the fyke nets, representing fish moving westward, usually recording the highest catches.

The appearance of young Arctic cisco in the Prudhoe Bay region on 20 August was the earliest on record. Previous studies indicate virtually no recruitment in 1981 and 1982 (Griffiths and Gallaway 1982; Griffiths et al. 1983), although Critchlow (1983) reports 31 Arctic cisco <100 mm caught at West Dock between 25 and 30 September 1982. In 1983, a moderate influx of small (<100-mm) Arctic cisco began on 27 August (Woodward-Clyde Consultants 1983). Subsequent studies have demonstrated this year-class to be weak relative to the 1979 year-class (Moulton et al. 1986). In 1984, recruitment was again virtually nonexistent, with less than 20 small Arctic cisco caught in the Prudhoe Bay region in mid-September (Moulton et al. 1986).

Larger fish were dominant in the first catches of age-0 Arctic cisco in Colville Delta fyke nets as indicated by a decrease in the size mode of fish from 70 to 74 mm for 26–30 August to 65–69 mm in the following 2 weeks (Fig. 3). Thus, the date of first capture at sampling stations along the Beaufort Sea coast, timing and duration of peak catches, occurrence of higher catches in eastern-oriented fyke nets, and presence of larger age-0 fish in first catches provide evidence for a westward movement of age-0 Arctic cisco from the Mackenzie River to the Colville River in 1985.

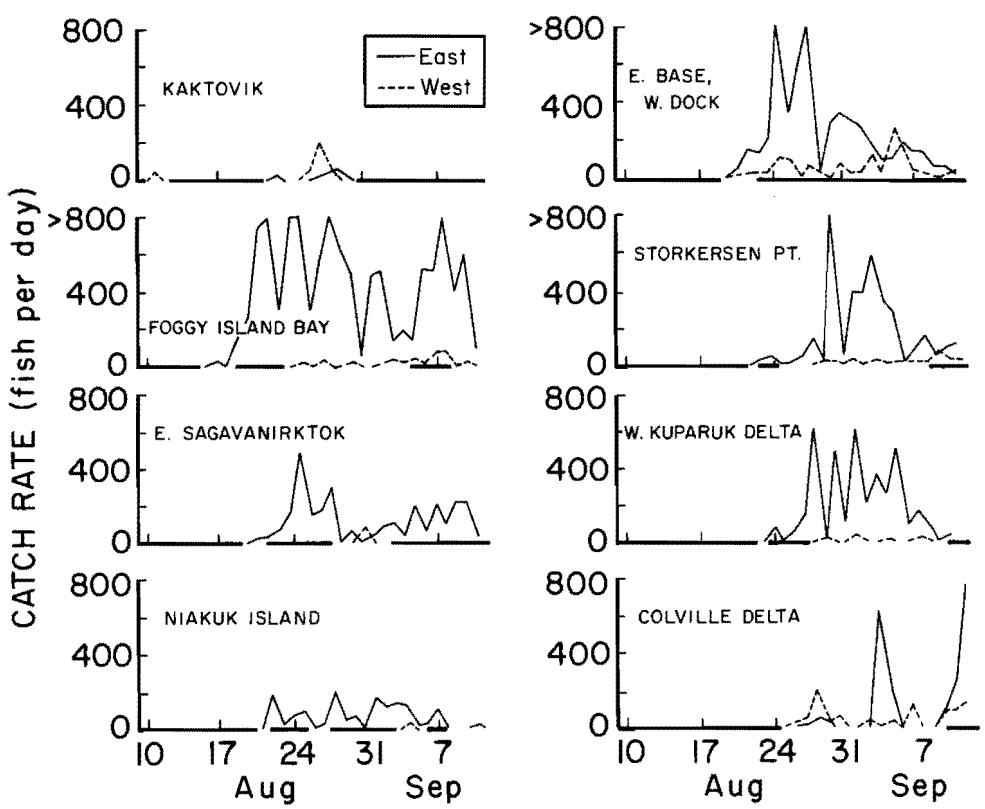

Figure 2. Catch rate (number per 24 hr) of small (<100-mm) Arctic cisco at locations between Kaktovik and the Colville Delta. Sampling at Kaktovik was not continuous from the first catch shown (data from Envirosphere [1986] and this study).

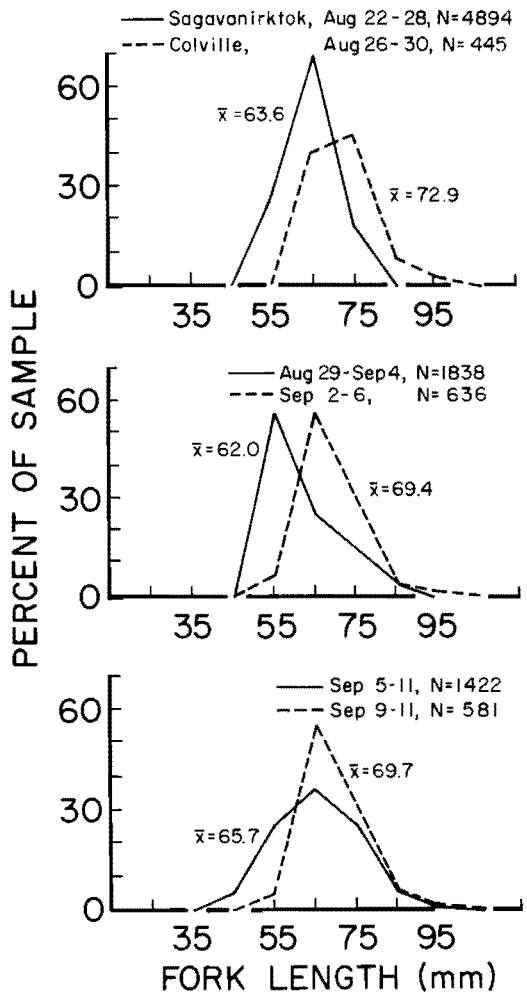

Figure 3. Size distribution of young Arctic cisco in the Colville and Sagavanirktok Deltas, late summer 1985 (Sagavanirktok data from Envirosphere [1986] data appendix).

It has been hypothesized that many of the summer movement patterns of anadromous fish in the Beaufort Sea coastal region are controlled by wind patterns during the brief open-water season (Woodward-Clyde Consultants 1983; Moulton and Fawcett 1984; Moulton et al. 1986). During 1985, the period of greatest fish movement (i.e., early July–late Aug.) was dominated by persistent easterly winds, with a few brief reversals to westerly winds (Fawcett et al. 1986). It is apparent that these persistent easterly winds assisted the observed westward movement of small Arctic cisco. Gallaway et al. (1983) suggested that under average summer wind and current conditions (5 and 15 cm/sec, respectively), passive drift of 70–110 mm Arctic cisco from the Mackenzie River to the Colville River would be accomplished in 35 days, or about 12.8 km/day. This rate is similar to the rates calculated for the movement of fish in 1985 (Table 1).

A comparison was made between the size distribution of age-0 Arctic cisco in the Colville Delta and the Sagavanirktok Delta using Sagavanirktok data from Envirosphere (1986) (Fig. 3). Although all differences in mean size between the two areas were significant (t-test, α = 0.05), the differences between age-0 fish were greatest in the first week with the difference decreasing in the following 2 weeks. The indication is that small fish continued to move into the Colville, thus reducing the apparent differences. The pattern again indicated that larger individual fish were in the vanguard of the migration along the coast. It is apparent, however, that the smallest of the group (45–55 mm) were still underrepresented in the Colville Delta when sampling ceased.

In 1986, additional information was obtained that indicated Arctic cisco movement between the Colville and Mackenzie regions is much greater than previously documented. In 1986, two fyke nets were deployed by Fisheries and Oceans, Canada at Kay Point and fished from late June to early September (W. Bond, Fisheries and Oceans, Canada, pers. comm. 1986). This was the first time that fyke nets had been a primary sampling method in the Canadian Beaufort Sea. Eight Arctic cisco tagged in the Prudhoe Bay region were recaptured. The fish ranged from 350 to 387 mm when recaptured—five had been at large for 1 year, one for 2 years, and two for 5 years. The two fish at large for 5 years were 305 mm, or approximately age-5 or -6 when tagged, and thus were approximately age-10 or -11 and had likely spawned at least once when recaptured (Fawcett et al. 1986; Moulton et al. 1986). Physical examination of the gonads indicated that some of the tagged fish had likely spawned the previous year (W. Bond, pers. comm. 1986).

CONCLUSIONS

A significant concern related to the hypothesized Mackenzie River origin of Arctic cisco is the effect of causeways near Prudhoe Bay and the Sagavanirktok Delta on the movements of young-of-the-year Arctic cisco. Assuming a Mackenzie River origin for Arctic cisco in the Colville River, successful migration to the Colville River is a critical life history phase that ensures continued Arctic cisco utilization of the Colville River delta and availability to local fisheries. The 1985 data indicate that the larger individuals of the young-of-the-year Arctic cisco successfully migrated past (or through the breaches of) the causeways, reaching rearing and overwintering areas in the Colville River delta with no apparent delay. Catch rates were still increasing when sampling was discontinued because of ice formation. The difference in size between age-0 fish in the Colville and Sagavanirktok Deltas was greatest during the first week of recruitment but decreased by the end of sampling. Environmental conditions (e.g., persistent easterly winds) and possibly a strong year-class of age-0 Arctic cisco likely facilitated the move-

ment of young Arctic cisco from the Mackenzie River to the Colville River in 1985. While the data support the hypothesis that the migration of age-0 Arctic cisco from the Mackenzie River into the Alaskan Beaufort Sea can be explained through passive transport, the question arises as to why similar patterns are not seen for least cisco and broad whitefish, both of which are also abundant in the coastal region near the Mackenzie Delta. Arctic cisco have a greater affinity for offshore waters and higher salinity as compared to least cisco and broad whitefish (Moulton et al. 1986). It is apparent that the young Arctic cisco must selectively position themselves in offshore portions of the Mackenzie River plume so that they are vulnerable to the westward transport processes. Least cisco and broad whitefish, which are less tolerant of salt water, likely remain in coastal areas where they are less susceptible to being transported away from the Mackenzie region.

The Canadian catch of Arctic cisco tagged in the Prudhoe Bay region demonstrates that at least some Arctic cisco are moving east into the Mackenzie region as they mature. The previous lack of tag returns is likely a result of gear bias and low sampling effort.

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Genetic Analysis of Population Variation in the Arctic Cisco (*Coregonus autumnalis*) Using Electrophoretic, Flow Cytometric, and Mitochondrial DNA Restriction Analyses

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Abstract. This study is a genetic test of the hypothesis that all Arctic cisco that occur along the Canadian and Alaskan Beaufort Sea coast originate from a spawning stock (or stocks) associated with the Mackenzie River. Late summer samples of fish were obtained from coastal waters near Point Barrow, the Sagavanirktok River, and Phillips Bay, each of which can be considered coastal feeding habitat. Samples were also obtained in autumn from the Colville River delta, and two spawning site samples were taken from the Peel and Arctic Red Rivers, tributaries to the Mackenzie River. Genetic data indicated that the coastal and Colville River delta samples were composed of fish from multiple breeding sites, the spawning site populations were genetically uniform, and the spawning sites were genetically different from one another. These data are consistent with the "Mackenzie hypothesis" and do not provide evidence for a differentiated Alaskan stock. Furthermore, the data suggest that the Arctic cisco, like other anadromous fish such as salmon, show fidelity to their natal streams for spawning but disperse in the Beaufort Sea and at overwintering sites.

The Arctic cisco possibly originated as recently as 10,000 years ago when the Wisconsin glacier that covered the Mackenzie River receded. The Yukon River Bering cisco population, which is only slightly different genetically, possibly gave rise to the Mackenzie River Arctic cisco population either as a result of stream capture or chance migration. This explains the difficulty for fisheries biologists to easily identify individual fish to species but also suggests that genetic approaches to species and stock identification are useful.

INTRODUCTION

The deltas of the Mackenzie River in the Canadian Northwest Territories and the Colville River on the Alaskan North Slope are known to support large overwintering populations of the Arctic cisco, *Coregonus autumnalis* (Gallaway et al. 1983). These river systems were therefore thought to represent the principal source of this commercially important species. In the Mackenzie River system, spawning migrations have been observed in the Peel, Arctic Red, Great Bear, Mountain, and Liard Rivers (Hatfield et al. 1972; O'Neil et al. 1981; Gallaway et al. 1983; McLeod and O'Neil 1983). Similar runs have not, however, been documented in the Colville River system. These observations led Gallaway et al. (1983) to propose their "single stock" hypothesis, that all North Slope cisco populations are derived from one (or more) breeding stock(s) associated with the Mackenzie River system. By this hypothesis, Alaskan populations are replenished regularly by cisco transported there from Canada by alongshore oceanic currents. An alternative hypothesis suggests that the North Slope and Mackenzie Delta populations represent distinct breeding stocks with little exchange ("two stock" hypothesis). The "single stock" hypothesis is appealing, but the evidence presented to support it has been largely circumstantial. It has nonetheless gained widespread credence in Alaska, and has become a principal criterion for assessing the impact of coastal developments on the North Slope. In particular, the potentially disruptive effects of an extended offshore causeway on the alongshore dispersal of Arctic cisco from Canada, and hence on the Alaskan cisco fishery, have been a major concern. A quantitative test of the hypothesis is therefore in order.

To test the hypothesis that Alaskan and Canadian stocks are distinct, we have measured the extent of genetic relatedness among populations of cisco collected from various points along the Yukon coast and North Slope. As a first approximation, the "two stock" hypothesis would be favored by a demonstration of genetically differentiated populations associated with the Alaskan and Canadian river systems. Any markers identified could then

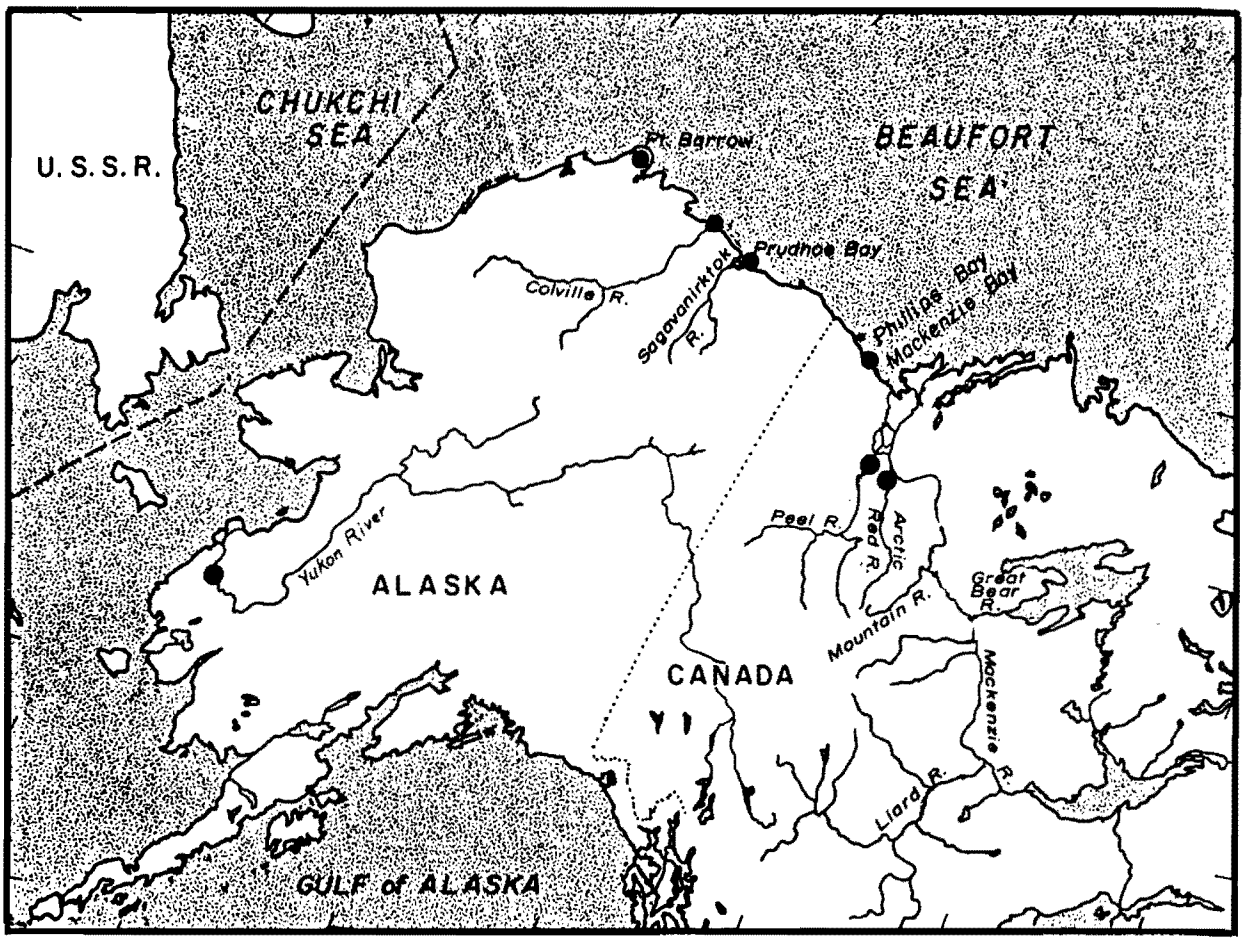

Figure 1. Sampling locations for Arctic cisco (*C. autumnalis*) and Bering cisco (*C. laurettae*) used in this study.

be used to measure the extent of mixing (as a result of gene flow) between these stocks. Alternatively, a demonstration of genetic similarity between these populations would be consistent with the "single stock" hypothesis. In this case, it would then be of interest to (1) ascertain if there were one or several discrete stocks in the Mackenzie system, and (2) if there were several Mackenzie stocks, determine in what proportions they were represented in the Alaskan fishery.

A morphologically similar species, the Bering cisco (*C. laurettae*), also was examined to allow us to measure the relative magnitudes of inter- and intraspecies genetic differentiation. The Bering cisco is found primarily along the Bering Sea coast of Alaska, and its distribution overlaps that of the Arctic cisco between Point Barrow and the Colville River (McPhail 1966).

METHODS

Study Area

Collections of Arctic cisco from the Yukon coastal zone (Phillips Bay) were made 26–29 July 1985 (Fig. 1). Collections from the Mackenzie River drainage were made in September 1985. We were successful in obtaining specimens from the Peel and Arctic Red Rivers but were unable to obtain fish from the lower and middle mainstream regions of the Mackenzie or from the Liard River. In Alaska, samples were obtained from both the Sagavanirktok and Colville River deltas (two samples from the latter) as well as from near Barrow, Alaska. A sample of Bering cisco from the Yukon River also was obtained. Samples (whole fish, or liver and heart tissue) were either frozen or placed on ice, packaged, and shipped as soon as possible from the field to the laboratory.

Protein Electrophoresis

All gels were made to 12.3 percent with 1:1 Connaught, Electrostarch, lots #410-1 and #392, respectively. Running and staining conditions followed or were slightly modified from Harris and Hopkinson (1976) and Selander et al. (1971). Table 1 lists the loci scored and the buffer systems used in the analyses. In addition to the 28 loci listed in Table 1, another 12 systems (at least 18 loci) were assayed that did not yield genetically interpretable results. Many of these loci were variable and some of the variation was observed as occurring between samples. It

Table 1. Loci scored and electrophoretic conditions used. Pairs of paralogous loci are denoted from cathode to anode as 1, 2 and 3, 4. Tetrasomic expression occurs for some of these systems in other salmonids (Leary et al. 1984), but monomorphism may mask the expression of duplicated genes in *Coregonus* (as indicated by *).

Locus	Electrophoretic conditions used
Aconitase-1,2,3,4	A
*Alcohol dehydrogenase-1	D
Glycerophosphate dehydrogenase-1	A
*Hemoglobin-1	E
*Isocitrate dehydrogenase-1,3,4	A
Lactate dehydrogenase-3,4	C
*Leucine amino peptidase-1	D
*Malate dehydrogenase-1,3	B
Malic enzyme-3,4	A
Mannosephosphate isomerase-1	D
*Methylumbelliferyl acetate esterase-1	B
*Octanol dehydrogenase-1	C
*Phosphoglucomutase-3	C
*6-Phosphogluconate dehydrogenase-1	A
*Phosphoglucose isomerase-1,3,4	F
*Superoxide dismutase-1,3	C
*Xanthine dehydrogenase-1	C

A: Electrode—0.687 M Tris (hydroxymethyl) aminomethane (Tris), 0.157 M citric acid, pH 8; Gel—22.89 mM Tris, 5.22 mM citric acid, pH 8.

B: Electrode—0.223 M Tris, 0.086 M citric acid, pH 6.3; Gel—0.008 M Tris, 0.003 M citric acid, pH 6.7.

C: Electrode—0.3 M boric acid adjusted to pH 8.2 with NaOH; Gel—0.076 M Tris, 0.005 M citric acid, pH 8.7.

D: Electrode—0.05 M Tris, 0.05 M NaH_2PO_4, pH 8.3; Gel—0.005 M NaH_2PO_4, pH 8.3.

E: Electrode—0.1 M Tris, 0.00166 M EDTA, adjusted to pH 9.0 with boric acid; Gel—0.005 M NaH_2PO_4, pH 8.3.

F: Electrode—0.03 M LiOH, 0.19 M boric acid, pH 8.1; Gel—1:9 mixture of 0.05 M Tris, 0.008 M citric acid, pH 8.4, and electrode buffer.

is possible that sample degradation accounts for our inability to score consistently many of these loci.

Genotypic diversity was assayed among and within samples of Arctic cisco using Haldane's (1954) analogue to Fisher's exact test. This exact test for randomness of mating was chosen to alleviate problems that would have otherwise stemmed from statistically small sample sizes. Tests for genotypic disequilibria and subsequent Wahlund effects were performed for each sample, all possible pairwise fusions of samples, and selected multiple fusions of samples for alleles segregating at the α-glycerophosphate dehydrogenase-1 (α-Gpd-1) and mannosephosphate isomerase (Mpi) loci. Alleles were pooled or treated independently where appropriate. Tests were performed only in cases where an $\alpha < 0.10$ was included within the range of the genotypic probability distribution for a given sample size with allele frequencies of p and q. The overall significance of this approach was then evaluated by comparing the expected frequencies of genotypic disequilibria obtained from the probability distributions with the observed frequencies of genotypic disequilibria.

Mitochondrial DNA

Mitochondrial DNA was prepared from 0.5–1.0 g of liver from each individual. Crude mtDNA isolates were prepared essentially by the methods of Wright et al. (1983). The mtDNAs were further purified by banding in cesium chloride–propidium iodide gradients in a Beckman TL-100 ultracentrifuge at 100,000 rpm from 5 hours to overnight (Carr and Griffith 1987). The mtDNA was collected and the banding was repeated once. The samples were then dialyzed extensively to remove the dye and cesium salt. The purified samples were then digested with various type-II restriction endonucleases (see Results) (Fuchs and Blakesley 1983), and the resulting fragments were end-labeled with ^{32}P-nucleoside triphosphates (Brown 1980). The labeled fragments were separated by electrophoresis through 1.2 percent agarose gels in Tris–EDTA–acetate buffer (90 V for 3 hr) or 3.5 percent polyacrylamide (BIS 1:20) gels in Tris–borate buffer (300 V for 6 hr) (Maniatis et al. 1983). The gels were then baked onto filter papers and autoradiographed.

Of the more than 100 specimens prepared, less than half (42 total) yielded mtDNA pure and/or intact enough for reliable restriction analysis (see Results). At least two problems were apparent. First, field collections are often made under less than ideal conditions, and specimens and tissues are often frozen either not soon enough or not cold enough. Prompt freezing (within 1–2 hr) in liquid nitrogen seems to be imperative in such field collections. Second, the tissue homogenates frequently contain large quantities of fat, which appear to reduce markedly the yield of both proteins and nucleic acids.

Flow Cytometry

Kidney tissue was removed from whole fish after thawing and prepared for flow cytometry (Bickham et al. 1985). Tissue was minced in Hanks' Balanced Salt Solution (Hanks' BSS) with scissors and scalpel until a single cell suspension was obtained. The cells were washed five times in fresh Hanks' BSS and subsequently fixed at least 24 hours in a solution of ethanol and Hanks' BSS (1:1 v/v). Aliquots of cells were stained overnight in 2 ml of 0.005 mg/ml DAPI (4,6-diamidino-2-phenylindole) in 0.04 M $MgCl_2$, 0.1 M Tris adjusted to pH 8.0 with HCl. Nuclear fluorescence was measured on a Leitz MPV flow cytometer. Epi-illumination was with a 100 W mercury vapor bulb using an A2 filter cube, which allows illumination of the sample in the 340–380 nm wavelength range. Cells were run in staining solution. An internal standard, either chicken red blood cells or *Mus musculus* (C-57 BL, an

Table 2. Observed allele frequencies for two polymorphic loci in Arctic and Bering cisco.

	Mpi				α-Gpd-1			
Sample locality	*N*	A	B	C	A	B	C	D	*N*
Arctic cisco									
Phillips Bay	20	0.150	0.850	0.000	0.289	0.447	0.026	0.237	19
Colville River (1)	20	0.200	0.800	0.000	0.350	0.450	0.125	0.075	20
Colville River (2)	9	0.167	0.833	0.000	0.278	0.556	0.056	0.110	9
Sagavanirktok River	16	0.125	0.813	0.063	0.275	0.575	0.050	0.100	20
Arctic Red River	17	0.176	0.794	0.029	0.281	0.344	0.156	0.219	16
Peel River	16	0.344	0.625	0.031	0.300	0.500	0.100	0.100	15
Point Barrow	3	0.333	0.333	0.333	0.333	0.333	0.000	0.333	3
Bering cisco									
Yukon river	11	0.800	0.200	0.000	0.409	0.000	0.545	0.046	10

inbred strain) spleen cells, was used and the gain controls of the flow cytometer were adjusted so that the *Mus* cell peak was at channel 100 or the chicken cells were at channel 30 (Burton et al., in press).

RESULTS

Protein Electrophoresis

Twenty-three of 28 loci were monomorphic across all 116 individuals of both species sampled. Two loci, Mpi and α-Gpd-1, were variable and included three and four alleles, respectively (Table 2). Allele B for Mpi is the most common allele for all populations of Arctic cisco ranging in frequency from 0.85 (Phillips Bay) to 0.625 (Peel River). The Point Barrow sample consisted of only three individuals and, thus, frequency data for that population are not considered. Allele A is present in all populations and ranges in frequency from 0.344 (Peel River) to 0.125 (Sagavanirktok River). Allele C is the rarest and is not found in two populations (Phillips Bay and both samples from Colville River). It ranges from 0.063 (Sagavanirktok River) to zero (disregarding Point Barrow). The Bering cisco differs in having allele A as the most common allele, B as a minority allele, and C being absent.

Allele B is the most common form of α-Gpd-1 in Arctic cisco (Table 2) ranging in frequency from 0.575 (Sagavanirktok River) to 0.344 (Arctic Red River). Allele A is next most frequent (0.35 in Colville to 0.275 in Sagavanirktok River) followed by D (0.237 in Phillips Bay to 0.075 in Colville) and C (0.156 in Arctic Red River to 0.026 in Phillips Bay). Allele C is most common for Bering cisco (0.545) followed by allele A (0.409). Allele D is rare (0.046) and B, the most common allele for Arctic cisco, is absent.

Rare allelic variants of phosphoglucose isomerase (Pgi-3 and Pgi-4) were observed in most samples of Arctic cisco. Additionally, a putative null allele and a mutant for absence of Pgi-3,4 heterodimer formation was observed in the Arctic Red River sample. Bering cisco from the Yukon River appear fixed for the common Arctic cisco Pgi-3,4 alleles.

A rare allelic variant of isocitrate dehydrogenase (Idh) segregating at Idh-3 or Idh-4 was also observed in all Arctic cisco samples.

Table 3 lists percentage heterozygosity and polymor-

Table 3. Observed and estimated heterozygosity (H) and polymorphism (P) for Arctic cisco.

	Observed *		Estimated†	
Sample locality	H	P	H	P
Phillips Bay	0.034	0.08	$0.062 < H < 0.216$	0.30–0.44
Colville River (1)	0.030	0.08	$0.059 < H < 0.213$	0.30–0.44
Sagavanirkok River	0.028	0.08	$0.058 < H < 0.212$	0.30–0.44
Arctic Red River	0.033	0.08	$0.061 < H < 0.215$	0.30–0.44
Peel River	0.038	0.08	$0.065 < H < 0.218$	0.30–0.44
Point Barrow	0.038	0.08	$0.065 < H < 0.218$	0.30–0.44

* Observed values are based on two polymorphic loci (Mpi and α-Gpd-1) and a total of 25 assayed loci. They do not include Pgi.

† Estimated values are based on the two observed polymorphic loci (Mpi and α-Gpd-1) and six additional polymorphic but unscoreable enzyme systems (Cat, Est, G3pd, Pep, Sdh, and Pgi). Minimal estimates of H and P are derived from the assumption that eight loci are encoded by these six additional enzyme systems. Maximal estimates of H and P are derived from the assumption that these eight loci are duplicated. Average heterozygosity levels for these additional systems are estimated to lie between 0.150 and 0.500.

Table 4. Results of the exact test for genotypic disequilibria at α-Gpd-1 and Mpi conducted on all possible allelic combinations.

	Locus										
	α-Gpd-1										Mpi:
Sample†	a–x‡	b-x	c-x	d-x	a-b	a-c	a-d	b-c	b-d	c-d	a-b
C	ns§	ns	**§	ns	—	—	—	—	—	—	ns
S	ns	ns	ns	ns	—	—	—	—	—	—	**
B	—	—	—	—	—	—	—	—	—	—	—
A	ns	ns	—	ns	—	—	—	—	—	—	ns
Ph	ns	ns	**	ns	—	—	—	—	—	—	ns
P	ns	ns	ns	—	—	—	—	—	—	—	ns
C, S	ns	ns	**	ns	ns	—	ns	*§	—	—	**
C, B	ns	ns	**	ns	ns	*	ns	—	—	—	**
C, Ph	ns	ns	**	ns	ns	**	ns	**	ns	—	*
C, A	ns	ns	**	ns	ns	**	ns	**	ns	—	ns
C, P	ns	ns	**	ns	ns	**	ns	ns	—	—	ns
S, B	ns	ns	ns	ns	ns	—	ns	—	ns	—	**
S, A	ns	ns	ns	ns	ns	—	ns	—	ns	—	ns
S, Ph	ns	ns	**	ns	ns	—	ns	**	ns	—	ns
S, P	ns	ns	ns	ns	ns	—	ns	ns	**	—	ns
B, A	ns	ns	—	ns	ns	—	ns	—	ns	—	ns
B, Ph	ns	ns	**	ns	ns	—	—	**	—	—	ns
B, P	ns	ns	—	ns	ns	—	—	—	*	—	ns
A, Ph	ns	*	**	ns	ns	**	ns	**	ns	ns	ns
A, P	ns	**	ns	ns	ns	—	ns	—	ns	—	ns
Ph, P	ns	*	*	ns	ns	**	ns	ns	—	—	ns
C, S, B, A, Ph, P	ns	*	*	ns	ns	**	ns	**	**	ns	*
A, Ph, P	ns	**	**	ns	ns	**	ns	*	*	ns	ns
C, S, B	ns	ns	**	ns	ns	—	ns	*	ns	—	**

† C, Colville River (1); S, Sagavanirktok River; B, Point Barrow; A, Arctic Red River; Ph, Phillips Bay; P, Peel River.
‡ Allelic combinations. x, pooled alleles; Mpi allele B includes the rare allele C.
§ ns, not significant; *, $P < 0.10$; **, $P < 0.05$.

phism for six samples of Arctic cisco. Observed values are based upon 25 loci. Estimated values include loci encoded by an additional six polymorphic enzyme systems from which complete data sets are not available.

All deviations from Hardy-Weinberg equilibrium entailed a deficiency of heterozygotes. Significant genotypic disequilibria were observed in all sample comparisons except for each of the two spawning localities and two of the pairwise fusions—Sagavanirktok River, Arctic Red River and Point Barrow, Arctic Red River (Table 4).

Genotypic disequilibria within samples involved the α-Gpd-1 C and Mpi A and B alleles. In addition to these alleles, disequilibria involving the α-Gpd-1 A, B, and D alleles were observed with respect to the pairwise and multiple fusions of samples. With respect to pairwise and multiple fusions, genotypic disequilibria were variably distributed. α-Gpd-1 A vs. C and α-Gpd-1 B vs. C disequilibria were commonly encountered, and α-Gpd-1 B vs. D and Mpi A vs. B disequilibria occurred less commonly among the pairwise and multiple fusion samples. Significant genotypic disequilibria were not detected for α-Gpd-1 A vs. B, α-Gpd-1 A vs. D, α-Gpd-1 C vs. D, or α-Gpd-1 A vs. the remaining pooled α-Gpd-1 alleles.

Relative frequency comparisons of expected and observed genotypic disequilibria provided rough estimates that within the three oceanic samples, observed disequilibria occurred an average of more than five times that expected by chance alone. Among pairwise oceanic fusion samples, observed disequilibria occurred at least 6.4 times more than expected.

Mitochondrial DNA

The following hexaschizomeric endonucleases define 30 restriction sites in mtDNA from the Phillips Bay sample: *Eco*RI, *Hind*III, *Sst*I, *Hpa*I, *Bgl*II, *Xho*I, *Sst*II, *Cla*I, *Dde*I, *Nhe*I, *Ssp*I. These produce from one to five fragments each. Several other endonucleases did not cut cisco mtDNA. A survey of 12 Phillips Bay individuals showed no variation for the nine fragments defined by *Hpa*I and *Nhe*I. Accordingly, 10 of these same individuals were again analyzed using the four endonucleases *Hinf*I, *Hae*III, *Hha*I, and *Mbo*I. These enzymes with tetrameric recognition sites define approximately 100 restriction sites among them. No fragment differences that could be attributed to site-specific point mutations were detected in these 10 individuals for any of the endonucleases. Examination of the *Hha*I and *Mbo*I patterns of nine Colville

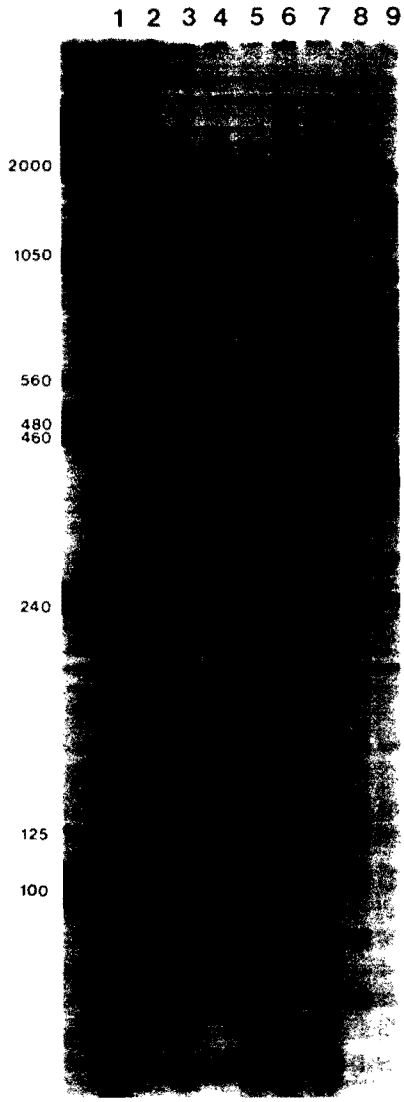

Figure 2. Length polymorphism in the mitochondrial DNA of Arctic cisco. Fish mtDNAs were digested with *Mbo*I, end-labeled with radioactive nucleotides, and electrophoresed in a 3.5 percent polyacrylamide gel. The gel was then dried onto filter paper and autoradiographed with Kodak RP film for 12 hours. The autoradiograph is shown. The leftmost lane shows end-labeled *Hind*III fragments of lambda phage and PM2 phage DNA, which serve as molecular weight standards (fragment sizes are given in base pairs). Lanes 1–9 show mtDNA from nine individual cisco collected at Phillips Bay, Canada. Thirty restriction fragments are detectable in each digest. The fragment size patterns were identical in all digests, except that in lanes 5 and 8 the largest (uppermost) fragment is about 100 base pairs larger than the corresponding fragment in other lanes. The change appears to be due to a difference in the size of the mtDNA molecules in these two fish.

River individuals and one each from the Arctic Red River and Sagavanirktok River samples showed these individuals to be identical with this pattern at 50 sites (Fig. 2).

Variation exists among individuals for the length of the mtDNA molecule. The largest fragment in the *Mbo*I digest is about 100 base pairs (bp) larger than the corresponding fragment in other fish in two out of 12 Phillips Bay fish and in three out of 17 Sagavanirktok River fish. The mtDNA of a single Arctic Red River fish is of the larger type (genotype B) as is one of 12 Colville River fish (Table 5). Figure 3 shows a partial sequence map of Arctic cisco mtDNA. The molecule is estimated to be 16.7 kilobases in length.

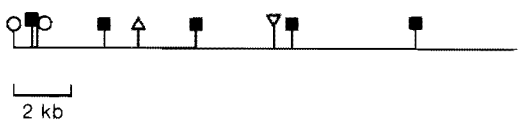

Figure 3. Restriction map of mitochondrial DNA from the Arctic cisco. Recognition sites for each endonuclease are indicated as follows: *Eco*RI = 0, *Hind*III = ■, *Sst*I = △, *Bgl*II = ▽. The linear map was derived from the circular molecule by assigning the zero position to one of the two *Eco*RI sites. The molecule represented here has an estimated circumference of 16.7 kilobase pairs. (Length polymorphism exists among individuals; see text.)

Flow Cytometry

DNA content data were obtained on 17 Arctic cisco and one Bering cisco (Table 6). The mean DNA content measurement for 16 Arctic cisco from the Colville River was 62.1 percent of the mammalian value. If we accept 7 pg per nucleus as representing the 2C value of the mammalian standard (channel 100 = 2C = 7 pg), this gives an estimated mean value of 2C = 4.35 for the Arctic cisco. The accuracy of this measurement is open to question due to the relatively large levels of variation found within and among samples. However, the mean value for the Arctic cisco agrees well with the mean value for 12 species of salmon (5.0 pg) reported by Johnson et al. (1987). The mean coefficient of variation for Arctic cisco was 9.3 percent, which is high for flow cytometry studies, and the standard deviation of the sample peak values was 15.4 channels. The peak values ranged from channels 28 to 80, but if individual 10 ($\bar{x}$ = 28) is disregarded as an outlier, the range is reduced to channels 40–80. Nonetheless, this range is significantly greater than is normally

Table 5. Distribution and frequency of mitochondrial DNA genotypes in four population samples of Arctic cisco. Genotype A is most common and possesses an *Mbo*I fragment that is approximately 100 base pairs smaller than the corresponding fragment in genotype B.

Population	*N*	Genotype A	Genotype B	% B
Phillips Bay	12	10	2	16.6
Arctic Red River	1	0	1	100.0
Colville River	12	11	1	8.3
Sagavanirktok River	17	14	3	17.6
Totals	42	35	7	16.6

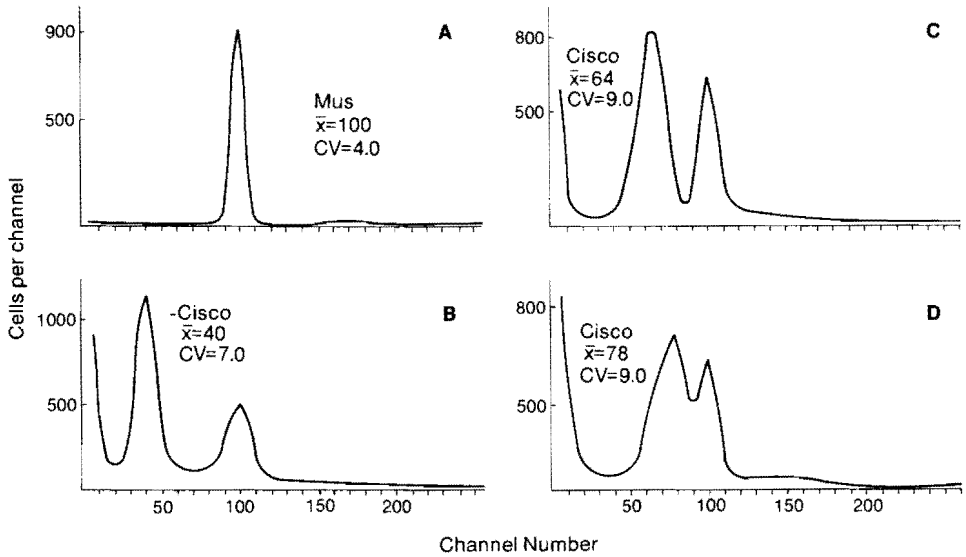

Figure 4. DNA flow histograms illustrating the range of variation in DNA content measurements for Arctic cisco from the Colville River. *Mus musculus* is used as an internal standard. (A) *Mus musculus* standard with G1 peak mean at channel 100. A total of 10,000 cells were counted in the G1 peak. In all subsequent figures the *Mus* peak is at channel 100. (B) Arctic cisco with G1 peak mean at channel 40 and *Mus* peak mean at 100. Total cells counted in cisco peak is 20,735. (C) Arctic cisco with peak mean at channel 64. Total cells in cisco peak is 19,149. (D) Arctic cisco with peak mean at channel 78. Total cells in cisco peak is 15,548. Note the overlap in the cisco and *Mus* peaks.

encountered in similar studies in our lab on animals as diverse as turtles and bats (Burton et al., in press). Figure 4 shows representative DNA flow histograms that illustrate the range of variation found in the species.

The estimated DNA content of a single Bering cisco was 100% of the mammalian value, or 2C = 7 pg. This is well outside the range of values obtained for the Arctic cisco. Because the Bering cisco peak overlapped with the *Mus* standard, chicken red blood cells were used as an internal standard (Table 6).

DISCUSSION

Levels of electrophoretic variation within and among populations of Arctic cisco (Table 3) appear to fall within the range reported for salmonid species (Utter et al. 1984) and for vertebrates in general. Although we did not find unique alleles or fixed differences sufficient to resolve the population samples into discrete stocks, such stocks might yet exist within the Mackenzie drainage. There is evidence of a unique null allele at the Pgi locus present only at low frequency in the Arctic Red River sample. Significant genotypic disequilibria, resulting from heterozygote deficiencies, were detected in the Sagavanirktok, Colville, and Phillips Bay samples and in the Arctic Red River and Peel River samples combined. Thus, the oceanic samples seem to be representative of a classic Wahlund effect (Wahlund 1928) in which the deficiency of heterozygous individuals is due to the pooling of individuals from different populations, whereas the spawning site samples (Arctic Red and Peel Rivers) are at equilibrium and somewhat differentiated from one another. What is clear is that no *strong* genetic differentiation, in the form of fixed allelic differences, has occurred among the populations sampled. This could be explained by sufficient dispersal among populations that divergence is prevented or by hypothesizing a recent origin of the species such that discrete populations have not had sufficient time to express significant levels of genetic differentiation. The latter hypothesis could result from either a recent origin of the species or a population (species) bottleneck. Moreover, the fact that Bering and Arctic ciscoes share the majority of their alleles and possess no fixed allelic differences indicates the two share a recent common ancestor. These hypotheses can now be considered in light of the mtDNA data.

Mitochondrial DNA restriction analysis has been shown to be a sensitive technique to demonstrate populational variation in a diversity of organisms such as sunfish (Avise and Saunders 1984) and deer (Carr et al. 1986). However, mtDNA sequence variation was not found in our samples of Arctic cisco. No variation that could be attributed to single-site base pair substitution was revealed either within or between Alaskan and Canadian populations. In a previous study of mtDNA variation in marine teleosts, populations of the skipjack tuna showed moderate levels of intraspecific restriction site polymorphism. This variation did not appear to be apportioned in any consistent way between Atlantic and Pacific populations (Graves et al. 1984). These authors attributed the absence of differentiation to extensive dispersal (gene flow) between oceans, and to the absence of discrete spawning areas. The latter

Table 6. Flow cytometric determination of DNA content in Arctic and Bering ciscoes.

Specimen	Sample $\bar{x}$	CV (%)	*Mus* $\bar{x}$	Chicken $\bar{x}$	Sample pg/nucleus
Colville (2) sample (Arctic cisco)					
Col2-1	43	7.5	100	—	3.01
Col2-3	74	11.0	100	—	5.18
Col2-4	58	13.0	100	—	4.06
Col2-5	40	7.0	100	—	2.80
Col2-6	56	7.5	100	—	3.92
Col2-7	70	11.5	100	—	4.90
Col2-8	78	9.0	100	—	5.46
Col2-9	80	9.5	100	—	5.60
Col2-10	28	6.0	100	—	1.96
Col2-11	72	8.5	100	—	5.04
Col2-12	71	7.0	100	—	4.97
Col2-13	71	11.0	100	—	4.97
Col2-14	69	10.5	100	—	4.83
Col2-15	46	10.5	100	—	3.22
Col2-16	74	10.5	100	—	5.18
Col2-18	64	9.0	100	—	4.48
Point Barrow (Arctic cisco)					
AK6353	45	6.5	100	—	3.15
Yukon River (Bering cisco)					
AK6350	100	12.5	—	30	7.00
Colville (2) sample					
	$\bar{x}$ = 62.1 (SD = 15.4)	$\overline{CV}$ (%) = 9.3			$\bar{x}$ = 4.35

condition at least does not obtain in cisco. Studies of freshwater fish have not revealed particularly low levels of intraspecific variation (Avise and Saunders 1984; Berg and Ferris 1984).

Variation in the physical structure of the mtDNA molecule does occur in the Arctic cisco. Earlier studies of mtDNA variation in mammals (e.g., Ferris et al. 1981) indicated that such large (≥100 bp) length polymorphisms were rare. Recent studies suggest that such variation may be more common in reptiles and amphibians (Densmore et al. 1985; Carr et al. 1987). Length polymorphism has not been previously reported in fish, although the level of resolution in previous studies may not have been adequate to detect changes on the order of 100 bp (Avise and Saunders 1984; Berg and Ferris 1984). Our findings are particularly reminiscent of Densmore et al. (1985), who found low levels of site-specific variation accompanied by relatively frequent length polymorphism among individuals within populations of parthenogenetic *Cnemidophorous* lizards. (These workers also reported extensive *intra*-individual length polymorphism, for which we have no evidence in cisco.) They suggest that such variation may arise rapidly within species, possibly by amplification of tandem repeats in the variable regions. For this reason, it would be important to characterize precisely the position and nature of the variable region in cisco.

Arctic cisco are unusual in combining a virtual absence of site-specific mtDNA variation and moderate levels of within- and between-population length polymorphism. This argues for a recent common (maternal) ancestor. If we assume that the rate of mtDNA sequence divergence in cisco is similar to that in mammals (about two substitutions per 100 base pairs per million years per pair of lineages) (Brown et al. 1979), there is an even chance of observing one substitution (site difference) among the roughly 100 sites examined after about 60,000 years. Similarly, there is less than a 5 percent chance that two lineages could persist separately as long as 250,000 years without one such observable site difference becoming fixed. This figure seems to be a reasonable upper limit on the age (time since last common ancestor) of the populations examined. This conclusion agrees generally with that from the data on protein-encoding loci presented above. The relatively lower level of mtDNA variation recalls the argument of Wilson et al. (1985) that founder events and transient bottlenecks will have a greater effect on mtDNA sequence variation than on nuclear sequences. This is in part because the maternally inherited mtDNA genome is effectively haploid.

If the elimination of site-specific variation indeed resulted from a recent bottleneck or founder event, then the observed length polymorphism must be of still more recent origin. This supports the suggestion of Densmore

et al. (1985) that such polymorphism can arise even more rapidly than site-specific variation in some cases. Further, if the origin were unique (as we assume), then the sharing of the polymorphism between Alaskan and Canadian populations indicates an absence of differentiation among these samples. Because the frequency of the minority genotype is approximately the same among the Phillips Bay (Canada), Colville River (Alaska), and Sagavanirktok River (Alaska) samples (Table 5), the "single stock" hypothesis of Gallaway et al. (1983) is supported. However, further examination of populations near their spawning sites will be necessary to determine the levels of genetic differentiation among spawning site populations within the Mackenzie River system.

By contrast with other genetic approaches, flow cytometry indicates a very high level of within-population DNA content variation (Table 6 and Fig. 4). Salmonid fishes are tetraploid as the result of an event that occurred as long ago as 25–100 million years, and most species of *Coregonus* have a diploid chromosome number of 2n = 80 (Allendorf and Thorgaard 1984). However, diploid numbers as high as 2n = 96 have been reported. It is in the nature of polyploids to be tolerant of gains and/or losses of chromosomes, which would result in variation of DNA content. The variation reported here was observed in oceanic samples, which presumably represent mixed populations from several spawning sites. Working back from this observation, it will be of interest to characterize the degree of DNA content (or karyotypic) variation in spawning sites in order to identify potentially useful genetic markers for stock identification.

The geological history of the Mackenzie River valley indicates that it was largely covered by the glacial ice sheet during the Wisconsin period, which ended 10,000 years ago. Because the Mackenzie River and its tributaries are the only spawning areas known for this species in North America, it is possible that the population is no older than 10,000 years. The geological history of this region as it relates to the fish fauna is discussed by McPhail and Lindsey (1970) and Lindsey and McPhail (1986).

Both the genetic data and geological history are consistent with the following scenario. After the retreat of the Wisconsin ice sheet a small number of Bering cisco dispersed farther east along the coast of the Arctic Ocean than the present range occupied by that species. These founders reached the Mackenzie River and initiated a breeding population at that site. Due to chance processes during the founder event, genetic variation for mtDNA was greatly reduced. The nuclear gene variation was maintained but significant allelic frequency shifts occurred as a result of the founder event. For the 10,000 years since the founder event, minimal morphological and genetic differentiation has occurred. A high degree of spawning-site fidelity has maintained the degree of genetic differentiation expressed in the founding stock. Geographic isolation has prevented the two species from becoming more similar, but insufficient time has elapsed for a high degree of differentiation to develop.

This scenario assumes the Bering cisco is the ancestral stock from which the Arctic cisco was derived. Because the Yukon River was not covered by the Wisconsin ice sheet, Bering cisco likely represent an older population that should be more genetically variable than the Arctic cisco. Thus, our model would predict higher levels of mtDNA variation and nuclear gene polymorphism in Bering as compared to Arctic cisco.

The relationship between Bering and Arctic cisco is uncertain. It is possible that Bering cisco represent a Pleistocene isolate that diverged from the more broadly distributed Arctic cisco. The Mackenzie River Arctic cisco population might have originated from Siberian populations of Arctic cisco. This could likewise have involved a genetic founder effect as described above. If this is true, then Siberian and North American Arctic cisco should be more similar to each other than either is to Bering cisco. This would be consistent with present taxonomy but would require dispersal of the founders across a greater distance.

Alternative scenarios could also explain the observed data. For example, Arctic cisco could have originated as the result of a stream capture shifting a spawning population from the headwaters of the Yukon River to the Mackenzie River. This is an attractive hypothesis because spawning site fidelity would be maintained in the founders. Further, the Peel River was tributary to the Yukon River during the last glaciation and now possesses a number of fish species with Yukon, rather than Mackenzie, affinities (Lindsey and McPahil 1986). Another alternative is that Arctic cisco are older than 10,000 years and persisted in a Pleistocene refugium such as the Peel River (McPhail and Lindsey 1970). This can be argued against because the electrophoretic data indicate a high degree of genetic similarity between the Arctic and Bering ciscoes, which is suggestive of a recent origin. Also, if the refuge population was small enough for drift to eliminate mtDNA variation and yet occurred over a long period of time (the lifetime of the Wisconsin ice sheet), then nuclear gene variation also should have been eroded. Considering all the information, we believe the first scenario mentioned above is most likely.

In conclusion, the data presented here, while they do not rule out the "two stock" hypothesis, are more consistent with the "one stock" hypothesis, in that oceanic Alaskan and Canadian populations are not strongly differentiated and share most genetic markers. Further, there is some evidence of multiple stocks within the Mackenzie River system. A more detailed comparison of populations within this system will be necessary to establish this point. Such studies should emphasize development of those markers that have been shown to be variable among populations examined thus far, namely (1) genotypic disequilibria at polymorphic electrophoretic loci, (2) mtDNA

length polymorphism, and (3) DNA content variation. It seems likely that such studies would reveal genetic information to address questions on the life history and management concerns for Arctic cisco.

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Biol. Pap. Univ. Alaska No. 24:123–130

"Noise" in the Distributional Responses of Fish to Environment: An Exercise in Deterministic Modeling Motivated by the Beaufort Sea Experience

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Abstract. Fishes in unstable habitats may forever seek their environmental preferenda without achieving them. Simulation of temperature-dictated movements of Arctic cisco suggests that lack of apparent correlation between synoptic distributions of these fish and temperature is a natural consequence of the complexity and dynamics of habitat–temperature distribution. More generally, the "noise" in fish-catch data may reflect not so much intractable stochasticity as the failure of empirical models to cope with the space–time dependencies inherent in such data. Because appropriate mechanistic models explicitly accommodate these dependencies, their judicious application could increase greatly the informational yield of fish-monitoring studies like those conducted in the nearshore Beaufort Sea.

INTRODUCTION

No experienced student of fish ecology doubts that fish movements and distribution are strongly influenced by such environmental variables as temperature, dissolved oxygen, currents, and light intensity. Yet, the precise role of these factors is difficult to infer from even the most carefully collected field data of the usual sort. One problem, of course, is that fish respond not to single environmental factors in isolation, but to the totality of environment. Even if the researcher could be sure that all important components of the environment are identified and properly measured, there remains the likelihood of complex interactions among components. Then, too, there are the usual doubts about the adequacy of the fish samples, in terms of size, frequency, and freedom from bias. Invariably, more and bigger samples are needed than reasonably can be obtained. This is because fish-catch data are notoriously "noisy," reflecting the large role of chance in the processes leading to fish distribution and apparent abundance.

There's the real culprit: Chance. If the researcher could measure all important environmental variables and collect truly adequate fish samples, he need only apply conventional multivariate regression analysis to unravel the effects of environment on fish distribution. Right? Before you agree too quickly, please consider our story[1] of Arctic cisco (*Coregonus autumnalis*) distribution in Quliuqtuat Bay on the Beaufort Sea coast.

[1] "Story" in the sense of definition S, The Compact Edition of the Oxford English Dictionary (Oxford University Press, 1971): "A narrative of real or, more usually, *fictitious* events . . ." (emphasis added).

A FISH STORY

Quliuqtuat Bay is typical of coastal waters along the Beaufort Sea coast of western North America. The Bay represents a seaward extension of the gently sloping coastal plain; the 2-m depth contour is almost 6 km offshore. During the arctic summer, strong winds drive the currents first one way and then another, at intervals of 2 to 4 days. Frigid, saline water from the open Beaufort Sea periodically invades the bay through gaps between the barrier islands and vies with warmer freshwater discharged from the Saglu River to dictate the bay's changeable environment.

In such habitats live several coregonine fishes, including Arctic cisco. Extensive sampling along the Beaufort Sea coast (e.g., Craig and Mann 1974; Craig and Haldorson 1981; Griffiths and Gallaway 1982; Critchlow 1983; Moulton et al. 1985; Envirosphere 1986) suggests that young Arctic cisco live mostly in the coastal band of warmer, less saline water. Temperature-preference experiments in the laboratory (Fechhelm et al. 1983) confirm that this fish prefers temperatures near 14°C (Fig. 1), which in coastal waters of the Beaufort Sea occur only in midsummer and then usually in association with river effluent.

Quliuqtuat Bay seemed an appropriate arena in which to settle, once and for all, the degree to which temperature governs distribution of young Arctic cisco in their natural habitat. To this end, we undertook an exhaustive sampling program. First, 25 stations were established at points 1 km apart on a five-by-five grid in Quliuqtuat Bay (Fig. 2). Then, at each of the 25 stations water temperature was monitored and a fyke net fished daily for 20 consecutive days during midsummer.

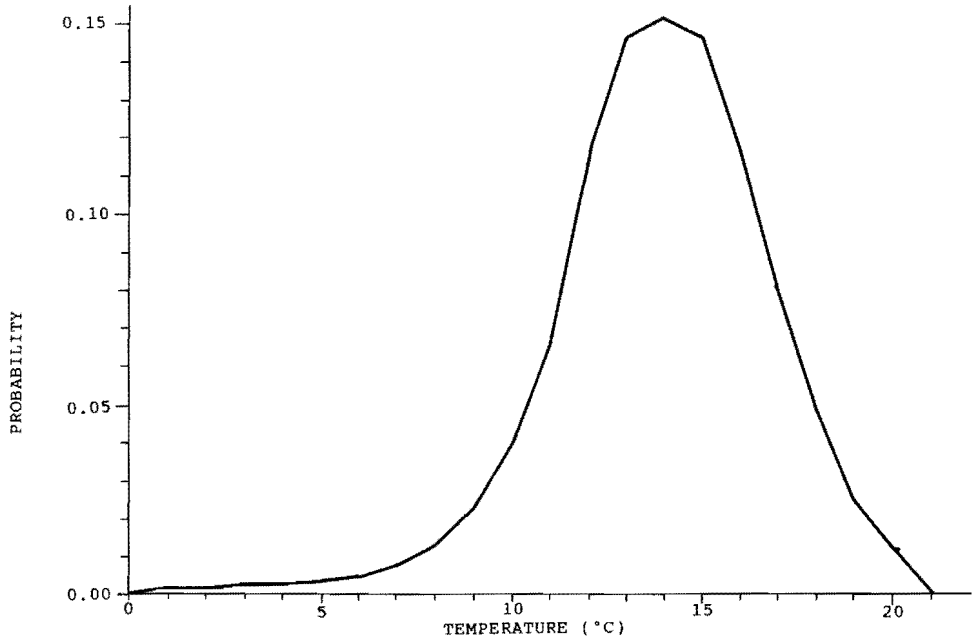

Figure 1. Idealized temperature–preference curve (probability density function) for young Arctic cisco. (Based on experiments in Fechhelm et al. 1983.)

The sequence of environmental events is evident from plots of the study area's isotherms at 2-day intervals (Fig. 3). At the beginning of the sampling period, strong northerly winds had driven cold oceanic water onshore, leaving the entire Bay uniformly at 3°C. Cessation of winds permitted the river discharge to form a typical thermal plume by day 2. The plume was better developed on day 4 but was deflected toward the southern shore by rising northeasterly winds and corresponding current drift. After a brief period of light westerly winds (day 6), the wind returned to the northeast and by day 8 had driven an intrusion of oceanic water through the Bay, cutting off a gyre of relatively warm water. By day 10, southwestward current drift preceding continuing northeasterly winds had compressed the river plume against the southern shore. Winds (and currents) were light and variable on day 12. Strong westerly winds and corresponding current drift then cut off a new "warm ring" and deflected the river plume eastward by day 14; persistent deflection of the plume resulted in marked compression of isotherms against the eastern shore of the bay by day 16. During the final days of the study, winds shifted to the northwest, diminished, and finally were calm by day 20.

What did young Arctic cisco do during this period of shifting thermal regimes? The pattern is made evident by considering events only at the central station, number 13. Temperature and catch of 10-cm-long Arctic cisco fluctuated drastically, but not in synchrony (Fig. 4). In fact, a plot of catch rate against temperature reveals the familiar lack of apparent correlation (Fig. 5). Only 10 percent of the variation in catch rate is attributable to variation in temperature, under the model presented in Figure 1.

From this result we must conclude that temperature had little demonstrable influence on the distribution of small Arctic cisco in Quliuqtuat Bay. Temperature's undoubted effects on physiology and behavior of the fish must have been overridden or masked by the operation of other variables or obscured by errors in sampling temperature, fish density, or both. Right? Wrong!—Variation in fish-catch rate was dictated entirely by variation in temperature.

THE "STORY" REVEALED

How can we be so confident, in the face of a straightforward regression analysis to the contrary, that temperature and temperature alone accounted for variation in our catch data? Our confidence derives from the knowledge that the story related above is just that—a "story." There were no catch data, because there was no field study in Quliuqtuat Bay. In fact, there is no Quliuqtuat Bay on North America's Beaufort Sea coast (to the best of our knowledge).

What we have described is a hypothetical study conducted via computer simulation. To be sure, the computer program incorporated as much realism and reason as we could muster. The temperature data are reminiscent of real observations in Alaskan coastal waters (e.g., Moulton et al. 1985). The model of Arctic cisco responses to temperature is that published in this journal 5 years ago (Neill et al. 1983); the published model produced results reasonably consistent with actual field data collected near the Waterflood Causeway (Prudhoe Bay) during summer 1981.

The model (Fig. 6) treats fish movement as a donor-

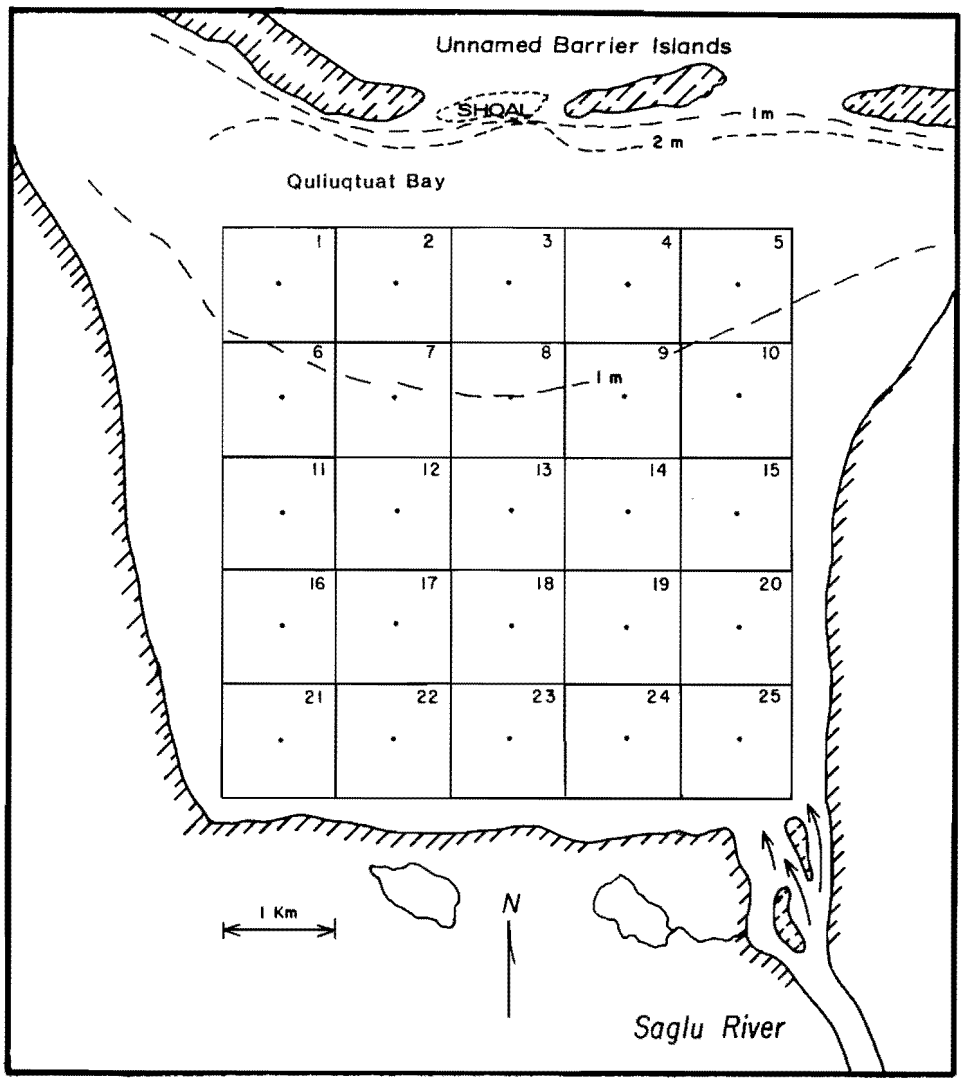

Figure 2. Quliuqtuat Bay, with locations of 25 sampling stations.

controlled drift process biased by the fish's temperature preference (which, for juvenile Arctic cisco, was measured experimentally by Fechhelm et al. [1983]). Considering two adjacent spatial locations (i and j), the fish continually move toward the location having the higher value of the ratio p:C, where p is the relative preference for the temperature (Fig. 1) and C the density of fish at that location; net rate of change in fish density (eq. 4 in Neill et al. 1983) is

$$\frac{dC_{ij}}{dt} = \frac{s}{X_{ij}} \cdot \left[\frac{p_i \cdot (C_i + C_j)}{p_i + p_j} - C_i \right],$$

where s is a temperature-dependent dispersal rate (maximally, the swimming speed observed experimentally by Fechhelm et al. [1983]) and X_{ij} is distance between locations i and j. At steady state, density of fish is directly proportional to p and, therefore, must be related to temperature in the same way as p.

The present implementation of the model involved 2,500 units of hypothetical fish density, initially distributed at 100 units per station. The computer program linearly interpolated station temperature between days (noon to noon) and evaluated fish-density flux on an hourly basis. The hourly values of density, averaged over the day, were output as daily "catch."

Plainly, catch of Arctic cisco vs. temperature at Quliuqtuat Bay's Station 13 (Fig. 5) bore little resemblance to the temperature-preference function (Fig. 1) driving the model! What explains the seemingly "sloppy" performance of our simulated fish? The explanation is not that other factors of environment interfered with or masked responses to temperature: The only environmental factor at work in Quliuqtuat Bay was temperature. Nor is the explanation a faulty sampling program: Samples both of fish density and temperature were flawless. Finally, chance was not the culprit: The model is deterministic, not stochastic.

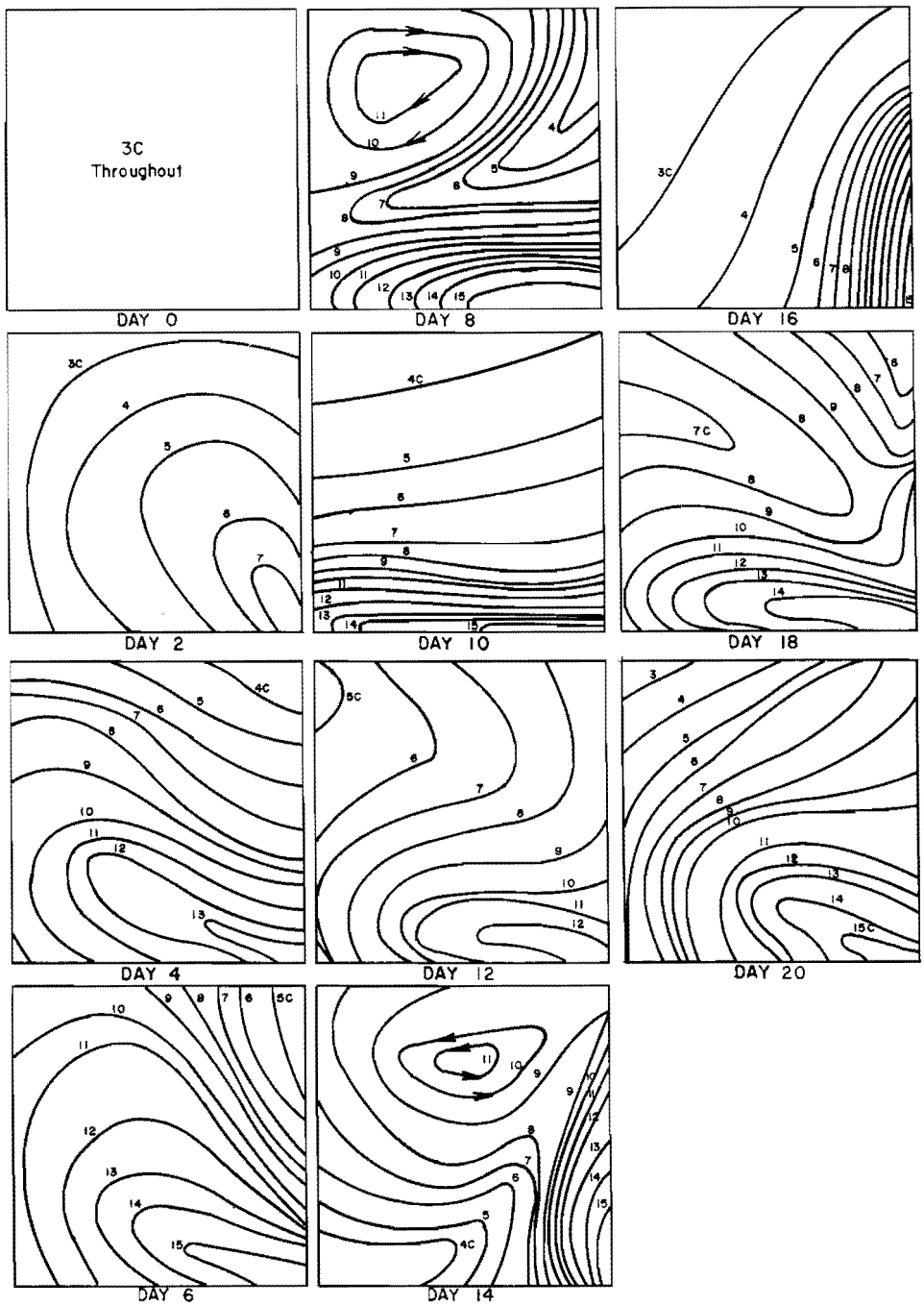

Figure 3. Thermal structure of study area at 2-day intervals over the 20-day study period.

The explanation is that all temperatures were not equally available and freely accessible to fish in Quliuqtuat Bay, and that small Arctic cisco simply could not swim fast enough to keep pace with the shifting thermal regime. Then, too, the relatively inferior thermal status of Station 13 caused the total number of fish "caught" there to underestimate the average density of fish in the Bay.

The explanation is made more explicit by erecting a model of conventional expectation, then resolving into components the "error" between that model's predictions and the simulation results. We began by specifying a model of conventional expectation. We decided that most of us, when confronted by a graph like that presented in Figure 4, casually compare the catch series with an intuitive model of the form

$$E(C) = CE = [p/\Sigma\, p(t)]\cdot\Sigma\, C(t),$$

where C is fish density at the station on a particular day, $E(C)$ is the expectation of C, p is the station's environmental value (from a graph like that in Fig. 1) on that

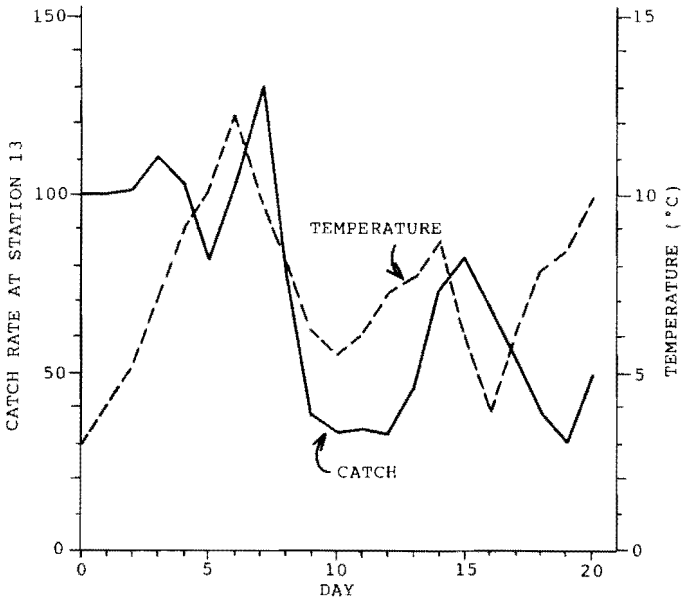

Figure 4. Time series of water temperature and catch of young Arctic cisco at Station 13 in Quliuqtuat Bay.

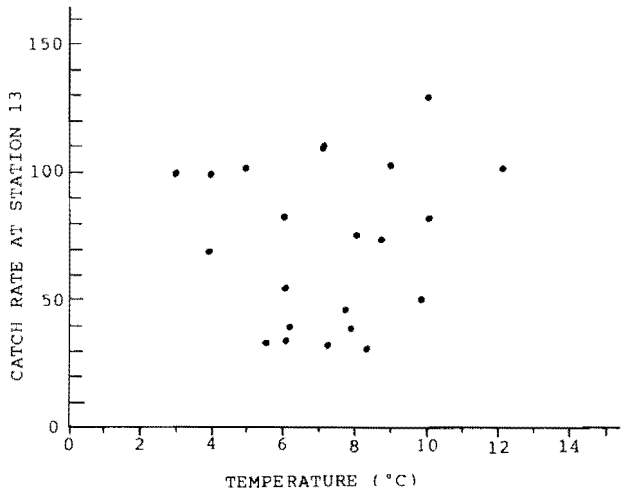

Figure 5. Catch of young Arctic cisco as a function of water temperature at Station 13 in Quliuqtuat Bay.

day, and the summations are over all days in the series. Underlying this model are the implicit assumptions that (1) the sampling station occupied a changing position in an array of environments equally available and freely accessible to the fish, and (2) the rate of change in environmental distribution was much slower than the fish could swim.

One or both of these assumptions was false for our simulated catch series at Station 13 in Quliuqtuat Bay: Fish density under the model of conventional expectation differed drastically from simulated density (Fig. 7). We evaluated the discrepancy by partitioning total "error" (CE–CSIM) into components due to (1) Station 13's misrepresentation of fish density in the system (CE–CETOT), (2) Station 13's misrepresentation of temperature availability in the system (CETOT–CEADJ), (3) restricted accessibility of temperature (CEADJ–CSS), and (4) inability of the fish to keep pace with temporal changes in the temperature distribution (distributional hysteresis, CSS–CSIM):

$$\begin{aligned} \text{CE–CSIM} = {} & (\text{CE–CETOT}) && \text{(Fig. 8A)} \\ & + (\text{CETOT–CEADJ}) && \text{(Fig. 8B)} \\ & + (\text{CEADJ–CSS}) && \text{(Fig. 9A)} \\ & + (\text{CSS–CSIM}), && \text{(Fig. 9B)} \end{aligned}$$

where CE is the conventional expectation of density as defined above; CSIM is simulated density; CETOT = $[p/\Sigma\, p(t)]\cdot 2{,}100$, 2,100 being the total (over all 21 days—days 0–20) "catch" expected at Station 13 had fish density at this site been average for the system; CEADJ = $[p/\Sigma\, p(s)]\cdot 2{,}500$, 2,500 being the total density of fish in the system on each day and the summation of p being over all 25 stations on each day; and CSS is steady-state density, computed by running the simulation to steady state for each day's temperature distribution, having begun with the distribution of CSIM on that day. The representation of distributional hysteresis as CSS–CSIM is obvious, but the interpretation of CEADJ–CSS as a measure

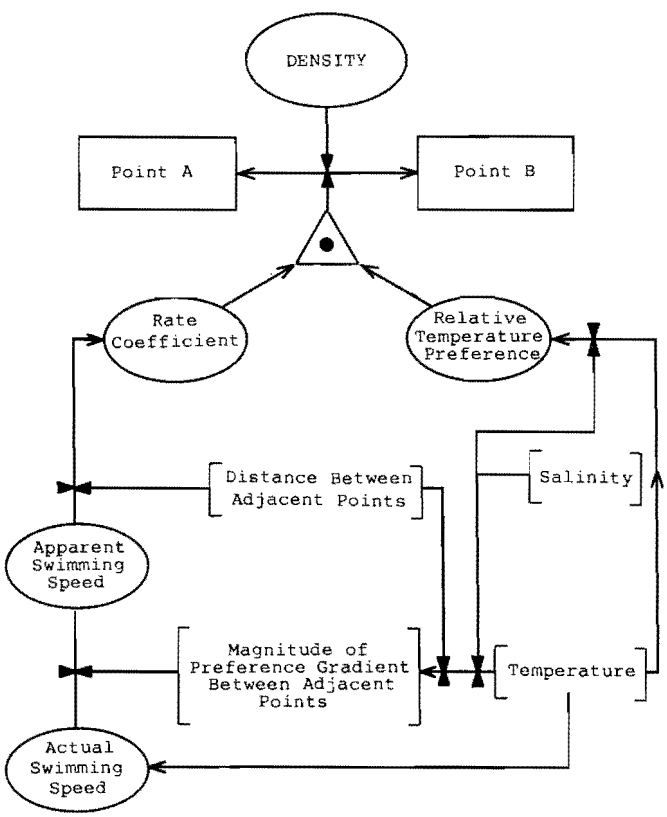

Figure 6. Conceptual model of fish movements between spatial points, with the rate of movement (density flux) being a function of environmental (brackets) and fish-specific (ovals) variables. (From Neill et al. 1983.)

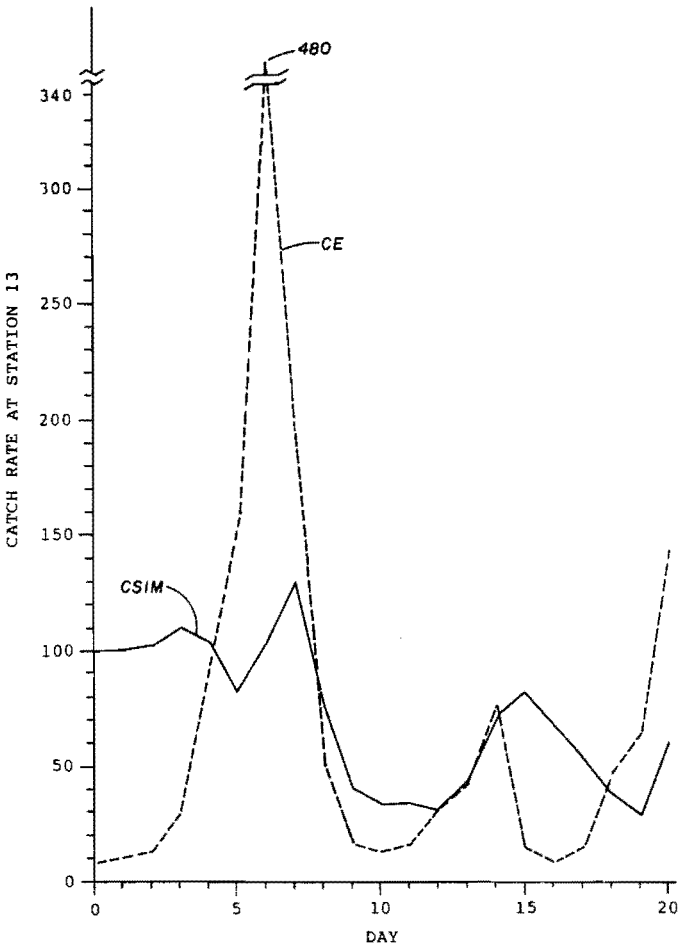

Figure 7. Total "error" between "catch" rate under the model of conventional expectation (CE) and that under the mechanistic simulation model schematized in Figure 6 (CSIM), on each day of the hypothetical study.

of restricted accessibility of temperature needs explanation. CEADJ is the expected density of fish at a particular station on a particular day, given that the thermal value of that station is adjusted for the availability of thermal values throughout the system. But movement of fish between two locations of equal value may be restricted by the existence of lower values at intervening locations. In the extreme, this leads to what Neill (1979) called environmental "trapping"—fish in habitat "oases" of relatively high environmental value (e.g., the warm gyres present in Quliuqtuat Bay on days 8 and 14) are trapped by surrounding habitat with lower values; similarly, high-value oases that appear de novo in low-value parts of the habitat may not be occupied because they are inaccessible. CEADJ is unaffected by these considerations; CSS reflects them. Thus, CEADJ–CSS is the appropriate measure of "error" associated with restricted accessibility of temperature.

How important, in our simulation, were the various "errors"? The "error" due to Station 13's misrepresentation of fish density in the system (CE–CETOT, Fig. 8A) was persistent, of course (being independent of temporal variation in the system), and amounted to 42 percent of average CSIM (=average CE). By far the dominant "error" was that due to Station 13's misrepresentation of temperature availability in the system (CETOT–CEADJ, Fig. 8B); average absolute magnitude of CETOT–CEADJ was 98 percent of average CSIM. Major discrepancies occurred during days 0–2, when higher temperatures were relatively rare, and during days 5–7 and 20, when higher temperatures were overrepresented. Absolute magnitudes of "errors" due to restricted accessibility of temperature (CEADJ–CSS, Fig. 9A) and distributional hysteresis (CSS–CSIM, Fig. 9B) averaged 13.5 and 26 percent, respectively, of average CSIM. We are reluctant to make more of these results because they reflect details of the specific thermal regime, which, after all, was only hypothetical.

THE MORAL

Our point in relating this exercise is not to argue that temperature is the sole factor influencing the distribution of Arctic cisco or any other fish; on the contrary, we are confident that fish *do* respond to the totality of environment, of which temperature is only one component—albeit, often an important one. Nor do we mean to belittle or discourage monitoring programs; such studies provide raw material useful for generating and essential for testing hypotheses about how fish–environment systems work in nature.

Our story's moral is this: Where a fish is located today depends partly on where it was yesterday and partly on environmental "lay of the land" between times and places. If environment is continually rearranged in space, as is so often the case in the Arctic, fish distribution is always in a transient state that may bear little relation to the fish's steady-state preferences. Therefore, a time-series of catch data, no matter how well attended by synoptic environmental data, may have little information content—unless a valid mechanistic model is available for interpreting those data. Unfortunately for all of us, distributional ecology is relatively long on data but short on models.

CONCLUSION

We who seek to understand the variation in fish distribution should set aside the familiar lack-of-effect scapegoats (e.g., effects of unknown variables, sampling error, and stochasticity of fish behavior) until we have considered that (1) the value (to the fish) of environment "here" depends on the value of environment "there," (2) a fish can't always get from "there" to "here," and (3) even when it can, the trip takes time. Proper consideration of these axioms requires both good data and good models.

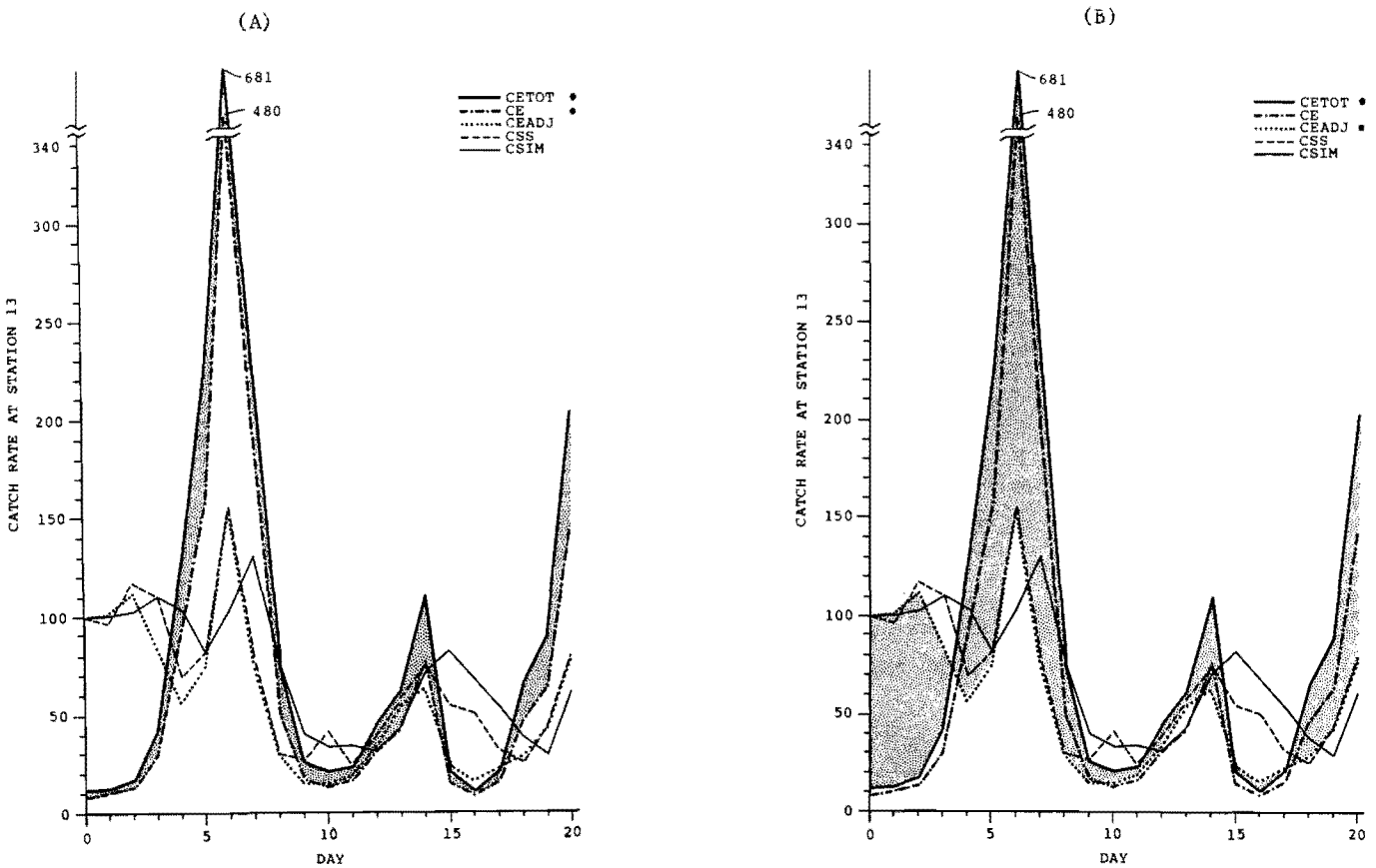

Figure 8. "Error" in simulated catch attributable to (A) Station 13's misrepresentation of fish density in the study area (CE–CETOT; see text), and (B) Station 13's misrepresentation of temperature availability in the study area (CETOT–CEADJ; see text).

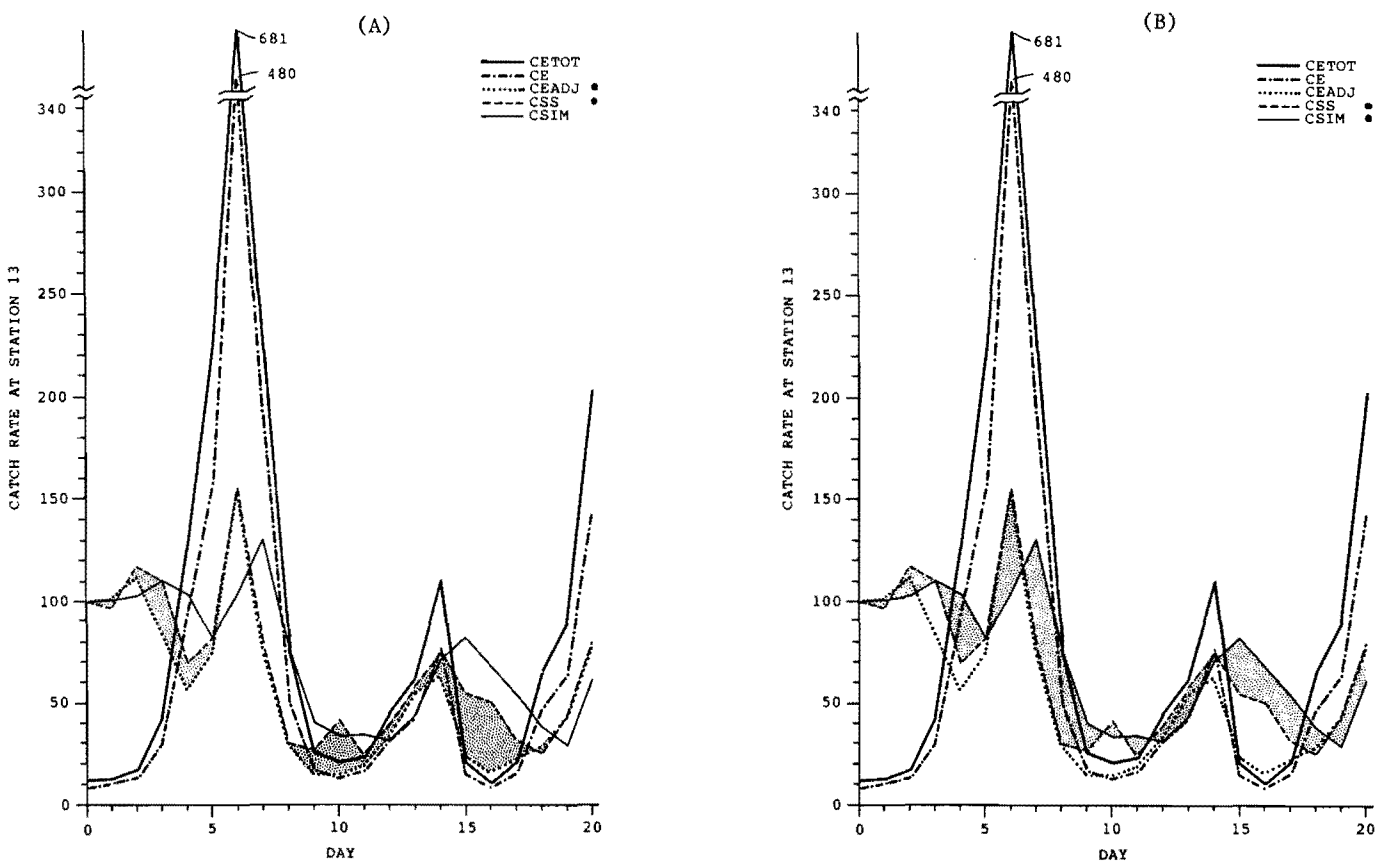

Figure 9. "Error" in simulated catch attributable to (A) restricted accessibility of temperature (CEADJ–CSS; see text), and (B) distributional hysteresis (CSS–CSIM; see text).

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Subsistence Fisheries at Coastal Villages in the Alaskan Arctic, 1970–1986

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Abstract. Subsistence fisheries in the Alaskan Arctic provide an important food source for the coastal communities of Barrow, Point Lay, Wainwright, Atqasuk, Nuiqsut, and Kaktovik. The total annual harvest (villages combined) is roughly 210,000 pounds of fish, which in terms of utilizable weight almost equals the villages' annual harvest of bowhead whales.

The fisheries concentrate on anadromous species (whitefishes, ciscoes, char, salmon) although freshwater species (grayling) are also taken. The species caught at each village differ, as would be expected based on distribution patterns of fishes in the study area. The fisheries are fairly well described in terms of timing and location but not harvest quantity. In some cases, the only available information about harvest quantity consists of a rough estimate made 15 years ago.

INTRODUCTION

Fish historically have been a vital food source for the Inupiat of the Alaskan Arctic. In modern times, fishing continues to be an important activity despite the rapid cultural and economic changes brought about since 1970 by the discovery and development of the North Slope oil fields. Fully one-third of the adult population in North Slope communities participated in fishing activities in 1977–1978 (Fig. 1).

The period covered in this report, 1970–1986, represents a time of transition of cultural values and patterns of subsistence use. Documentation of subsistence fisheries during this period has been sparse, however, with most available reports describing fishing only in general terms and often from a cultural perspective. There are few detailed accounts of actual quantities of fish harvested, and the information that is available is not generally known for two reasons: the data occur in widely scattered reports by government agencies and private firms, and people interested in subsistence information are often unaware that pertinent information may be "hidden" in the occasional scientific fish report.

The overall objective of the present study is therefore to assemble the available information and assess the current state of knowledge about modern subsistence fisheries at North Slope communities. The report focuses on the fish and fisheries themselves, i.e., what species are caught, how many, where, and when. This focus specifically precludes an analysis of the cultural or economic significance of the fisheries—these topics are described by others (e.g., Nielson 1977; NSB 1979a; Kruse et al. 1981; Jacobson and Wentworth 1982; Alaska Consultants et al. 1984; Braund and Burnham 1984; Galginaitis et al. 1984; Stern 1985).

METHODS

The study area is the North Slope of Alaska, from Point Lay to the US–Canada border on the Beaufort Sea (Fig. 2). Subsistence fisheries are examined at six coastal villages: Point Lay, Wainwright, Barrow, Atqasuk, Nuiqsut, and Kaktovik. These villages were selected because I had first-hand knowledge of them, and had conducted fish studies at most of them. Several villages south of Point Lay were not included.

This report is based on a literature review and discussions with people familiar with fish research conducted in the study area (see Acknowledgments). The intent was to collect fisheries information, particularly to search for "hard data" describing actual quantities of fish harvested. Original data have therefore been emphasized. For completeness, the literature search included many pre-1970 documents as well (e.g., Murdock 1884; Bean 1887; Hewes 1947; MacGinitie 1955; Sonnenfeld 1956; Wilimovsky 1956; Milan 1964; Spencer 1959; Foote 1965; Bane 1966; Hanson et al. 1966; Nelson 1966, 1969; Andersen 1982). In fact, only one pre-1970 report contained the kinds of quantitative data useful for this account.

In this report, the term "subsistence fishery" is used in its broadest sense, i.e., the personal use of locally caught fish for food. Some fish are also traded or sold to other villagers, but the degree to which this occurs is not known and therefore these fish are considered to be part of the subsistence catch.

This report concentrates on fishing areas of known and often traditional importance, but the reader should note two points. First, the studies described were typically 1 year or less in duration, so that annual variations in fish-

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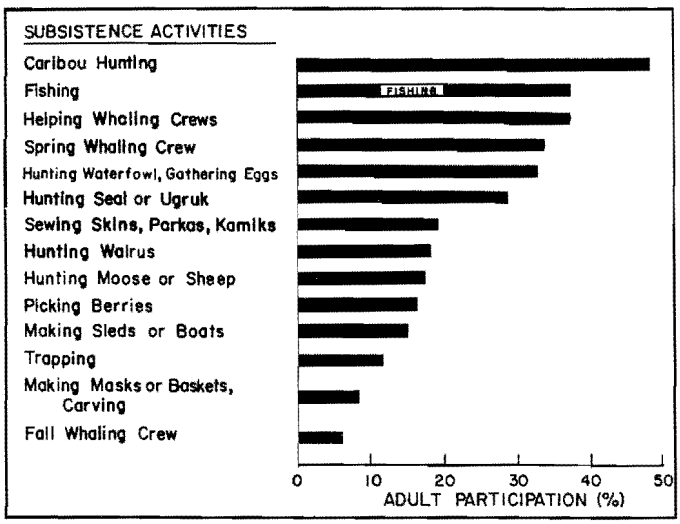

Figure 1. Proportion of adults from North Slope communities who participated in various subsistence activities in 1977–1978. The sample size was 290 adults from the villages of Point Hope, Wainwright, Barrow, Nuiqsut, Kaktovik, and Anaktuvuk Pass. Redrawn from Kruse et al. (1981).

ing patterns were not documented. Second, it is recognized that people may catch fish for their immediate consumption wherever they travel or hunt, which may include the entire North Slope when the subsistence-use areas of all the villages are viewed in total (Fig. 3).

The standardized unit of fish harvest used in this report is the total weight of the catch. Weights originally expressed as "dressed weights" have been converted to total weight according to the conversion factors used by the authors. Differences between total and dressed weights (about 20%) are not particularly significant given the imprecise methods used to approximate annual harvests in all studies.

Population sizes of the North Slope communities were obtained from Kruse et al. (1981) and the Alaska Department of Community and Regional Affairs (FY 1986 Revenue Sharing Program).

THE FISHES

Subsistence fishermen catch a variety of species in arctic waters (Table 1), but not all of these species are of equal value—some are discarded and others are not abundant throughout the study area. The principal species harvested (in terms of biomass) thus differ among the villages (Table 2).

Two features of the environment influence fish distributions in the study area and thus determine the kinds of fishes that are available to the various fisheries (Craig 1984a,b):

1. Proximity to the Bering Sea. The Chukchi Sea is a transition zone between the warmer, productive waters of the Bering Sea and the colder, less productive waters

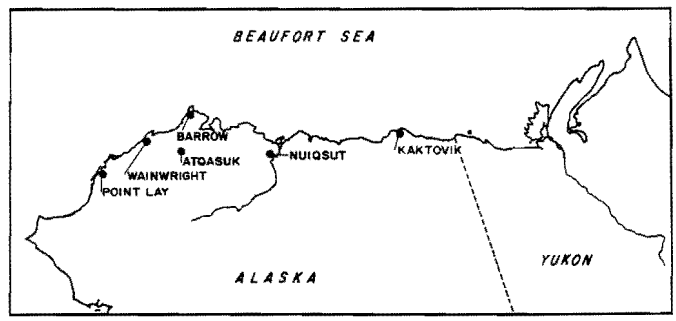

Figure 2. North Slope communities reviewed in this paper.

of the Beaufort Sea. Some southern species such as salmon and herring range northward into the northeastern Chukchi Sea but are scarce in the Beaufort Sea. Salmon are thus more common in subsistence harvests at Point Lay, Wainwright, and Barrow than at villages along the Beaufort coast.

2. Locations of anadromous fish streams. When anadromous fish enter the coastal waters of the study area, many do not range far from their natal rivers. Thus, the species composition and abundance of anadromous species in coastal waters generally reflect the proximity of the rivers from which the fish came. In this respect, the study area can be divided into three coastal regions with different fish species composition, as illustrated in Figure 4.

First, streams in the Chukchi region (Point Hope to Barrow) are generally small and of marginal significance for anadromous fishes. The relatively few anadromous fishes produced in this region (notably salmon) contribute to the subsistence fisheries at Point Lay, Wainwright, and Barrow.

Second, streams in the central part of the study area (Barrow to the Colville River) produce primarily whitefishes and ciscoes, which are prominent in the subsistence harvests at Barrow, Atqasuk, and Nuiqsut.

Third, streams in the eastern portion of the study area (Colville to the Mackenzie Rivers) produce primarily Arctic char. These char, together with migrant Arctic cisco from the Mackenzie River, constitute most of the subsistence catch at Kaktovik.

Although fish populations are distributed generally in accordance with these patterns, individual fish may disperse farther along the coastline. For example, fish tagged in Simpson Lagoon (Fig. 5) and Prudhoe Bay have been recovered from Barrow to the Mackenzie River.

General distribution patterns of the commonly harvested species are described below.

Anadromous Species

Anadromous species, whose life cycle includes both a freshwater and a marine phase, constitute by far the largest portion of subsistence harvests at North Slope villages.

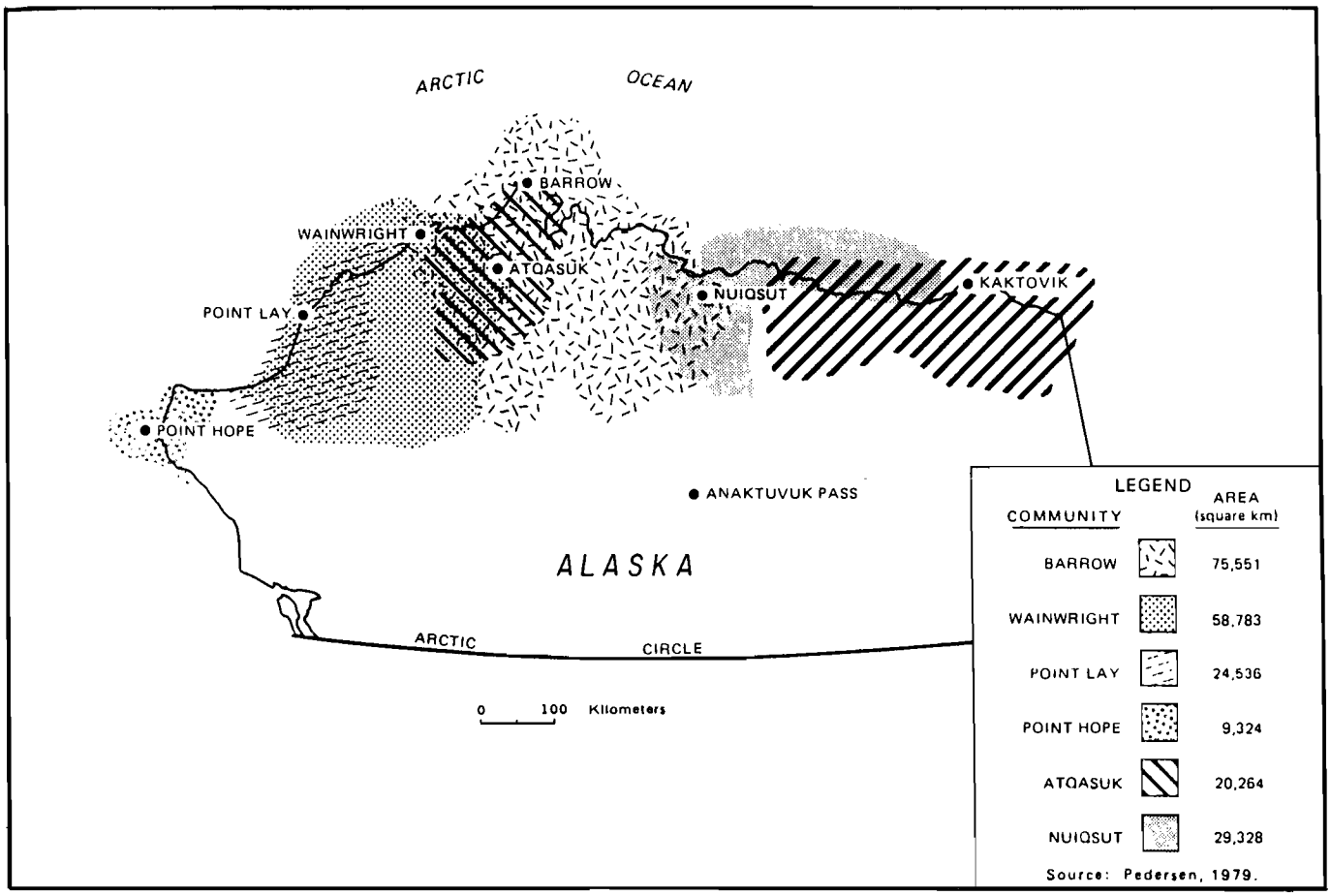

Figure 3. Subsistence-use regions for all resources used by each North Slope village. Source: Pedersen (1979).

The principal anadromous species caught are salmon, Arctic char, whitefishes, ciscoes, and rainbow smelt.

Salmon

Pacific salmon, though not very abundant in arctic waters (reviewed by Craig and Haldorson 1985), are most common along the coastline of the northeastern Chukchi Sea (Fig. 6). Only pink (humpback) and chum (dog) salmon occur with any regularity in the study area. Pink salmon are the most common species, accounting for 85 percent of all salmon caught in biological surveys from 1970 to 1984, followed by chum salmon (13%). "Silver salmon" are also caught, but this is a generic term that may be applied by subsistence fishermen to sea-run salmon of any species.

Small runs of pink salmon occur in several streams between Point Hope and Barrow, and perhaps in the Colville River. Their abundance in the study area is highly variable both seasonally and annually. Pink salmon display a cyclical pattern of abundance—they are much more abundant in even-numbered years than odd-numbered years, as is the general pattern for this species in western Alaska (Heard 1986). Their run timing in coastal waters usually extends from the last week in July through August, with peak numbers occurring during the first half of August.

Chum salmon are not often caught east of Point Barrow, although there is a small population that spawns in the Mackenzie River (McLeod and O'Neil 1983).

Arctic Char

In the study area, char are most abundant between the Colville and Mackenzie Rivers (Fig. 6), which accounts for their prominence in subsistence catches at Kaktovik. They are usually harvested in coastal waters from late June to September, but they are also caught at traditional inland fishing sites on the Hulahula River in fall and winter.

While in coastal waters, char range east and west along the Beaufort Sea coastline and thus individual stocks become mixed. Tagging studies have shown, for example, that char caught at Kaktovik originated from several North Slope rivers (Sagavanirktok, Canning, and Firth Rivers). Thus, the summer harvest of char from coastal waters distributes the fishing pressure among several stocks,

Table 1. List of commonly caught fishes in the study area.

Common name	Scientific name	Inupiat name*	Weight (lb)†
Anadromous species			
Chum salmon	*Oncorhynchus keta*	iqalugruaq, iqaluruaq	6.0–9.0
Pink salmon	*O. gorbuscha*	amaqtuq	2.0–3.1
Arctic char	*Salvelinus alpinus*	iqalukpik	0.9–4.0
Whitefish			
Broad whitefish	*Coregonus nasus*	aanaakliq, aanaaliq	1.2–3.9
Humpback whitefish	*C. clupeaformis*	pikuktuuq	1.4–2.3
Arctic cisco	*C. autumnalis*	qaaktaq, qaatag	0.8–2.0
Least cisco	*C. sardinella*	iqalusaaq	0.5–0.9
Bering cisco	*C. laurettae*	qaaktaq, tipuk	1.1–2.2
Rainbow smelt	*Osmerus mordax*	ilhuagniq	0.15–0.25
Marine species			
Pacific herring	*Clupea harengus*	uqsruqtuuq	0.3–0.4
Arctic cod (tomcod)	*Boreogadus saida*	iqalugaq, uugaq	0.05–0.13
Saffron cod (tomcod)	*Eleginus gracilis*	uugaq	0.06–0.31
Capelin	*Mallotus villosus*	panmaksraq, panmagriq	0.02–0.04
Fourhorn sculpin	*Myoxocephalus quadricornis*	kanayuq	
Arctic flounder	*Liopsetta glacialis*	nataagnaq, puyyaqiaq	
Freshwater species			
Arctic grayling	*Thymallus arcticus*	sulukpaugaq	0.3–1.7
Lake trout	*Salvelinus namaycush*	igalukpak	2.7–14.4
Burbot (lingcod)	*Lota lota*	tittaaliq	2.0–10.0
Round whitefish	*Prosopium cylindraceum*	savigunaq, aanaaliq	0.5–0.9

* Sources: Schneider et al. 1980; Nelson 1981; Jacobson and Wentworth 1982; Pedersen et al. 1985; Stern 1985; George and Nageak 1986.

† Typical whole weight of subsistence-caught fish based on numerous sources.

whereas fishing in the Hulahula River focuses the pressure on a single small stock.

Arctic Cisco

The Arctic cisco, a favored food fish because of its fatness, is harvested primarily at Kaktovik and Nuiqsut. The coastal distribution of this species is similar to that of char (Fig. 6), but the sources of the two species differ. There are no known spawning areas for the Arctic cisco in Alaska, so it is thought that the Arctic cisco in the study area originate in the Mackenzie River (Gallaway et al. 1983). These authors suggest that a portion of the Mackenzie population migrates into Alaskan waters as juveniles and then remains for several years in the vicinity of the Colville River before returning to the Mackenzie River to spawn. Nuiqsut fishermen catch these Arctic cisco in fall when the fish gather in the Colville River to overwinter, and Kaktovik fishermen catch them as they migrate back to the Mackenzie in summer.

The number of Arctic cisco available to these fisheries is presumably directly dependent on the number of juveniles that migrate into Alaskan waters from the Mackenzie River (Moulton et al. 1986; Gallaway et al. 1989). This has important ramifications for the fisheries—low recruitment from the Mackenzie leads to low harvests in

Table 2. Primary species of fishes harvested at North Slope villages.

	Primary fish species harvested							
Village	Herring	Salmon	Rainbow smelt	Whitefish	Least cisco	Arctic cisco*	Arctic char	Grayling
Point Lay	+	+						+
Wainwright		+	+					+
Barrow		+		+	+	+		
Atqasuk				+	+			+
Nuiqsut				+	+	+	+	+
Kaktovik						+	+	

* Arctic or Bering cisco.

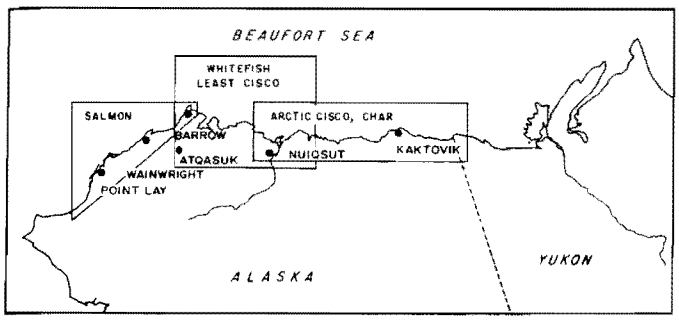

Figure 4. Principal species of anadromous fish harvested by coastal region.

Alaska several years later when the fish have grown large enough to be caught. Such fluctuations are reflected in the highly variable catch-per-unit-effort for Arctic cisco in Helmericks' commercial fishery in the Colville River delta (Fig. 7).

Other Anadromous Species

The rainbow smelt lives most of its life in marine waters but enters rivers in springtime to spawn. In winter these fish gather in Wainwright Inlet (lower Kuk River) where they are harvested by fishermen from Wainwright (Fig. 6). Smelt also congregate off the mouth of the Colville River in winter (Haldorson and Craig 1984), but there is no fishery for them there.

Other anadromous species important in subsistence catches are whitefishes (broad, humpback) and least cisco. These species do not disperse far in coastal waters (compared to Arctic cisco and char) and are therefore most abundant near their rivers of origin. Large numbers are caught at Barrow, Atqasuk, and Nuiqsut in summer and fall.

The Bering cisco also occurs in coastal waters between

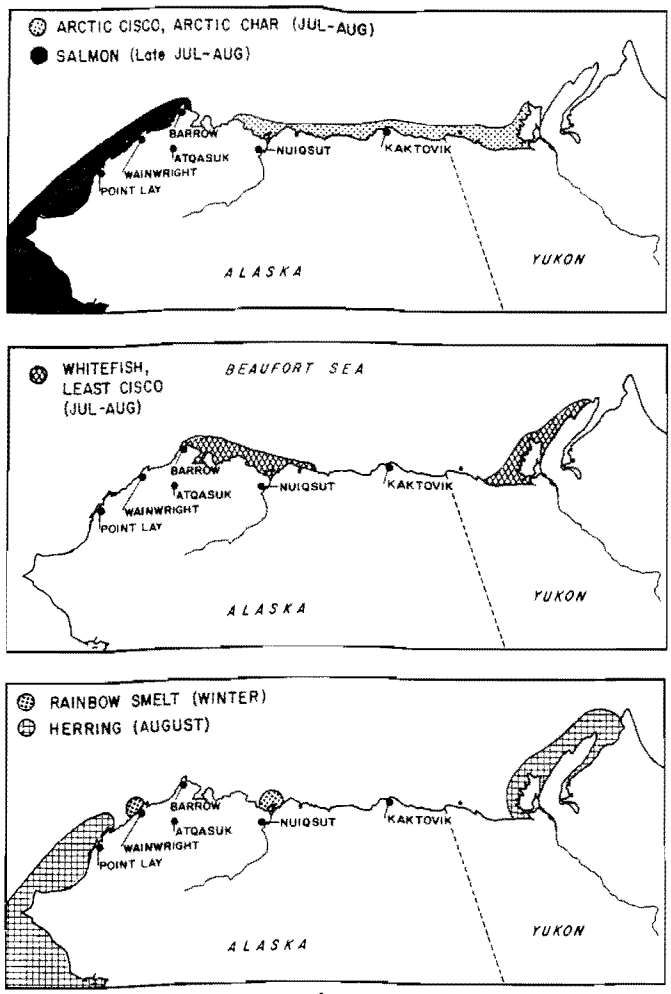

Figure 6. Coastal regions where anadromous fishes are most abundant (note that distribution limits are greater than these zones of abundance). The disjunct distribution of Arctic char south of Point Hope is not depicted.

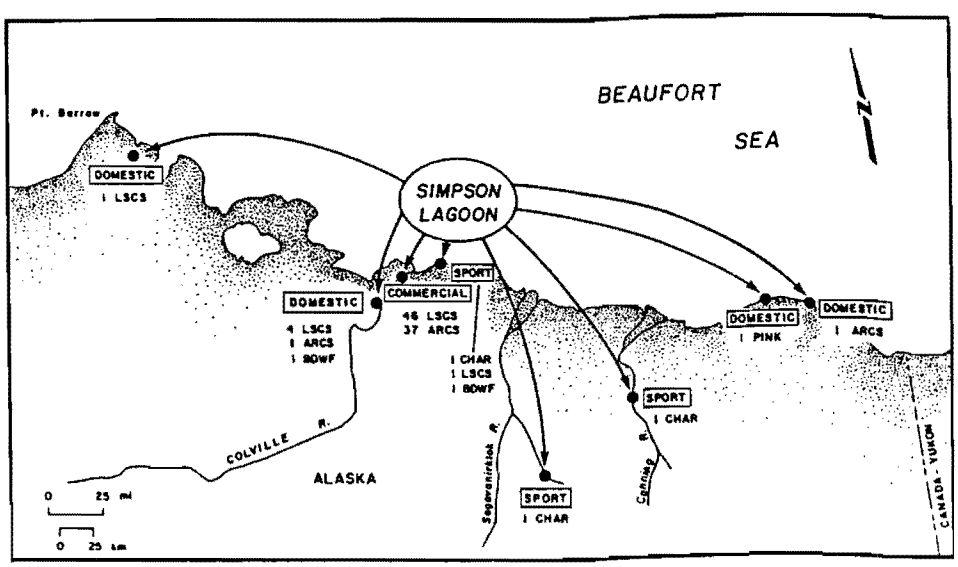

Figure 5. Fish tagged in Simpson Lagoon and recaptured in commercial, domestic, or sport fisheries. Abbreviations: ARCS = Arctic cisco; LSCS = least cisco; CHAR = Arctic char; BDWF = broad whitefish; PINK = pink salmon. Source: Craig and Haldorson (1981).

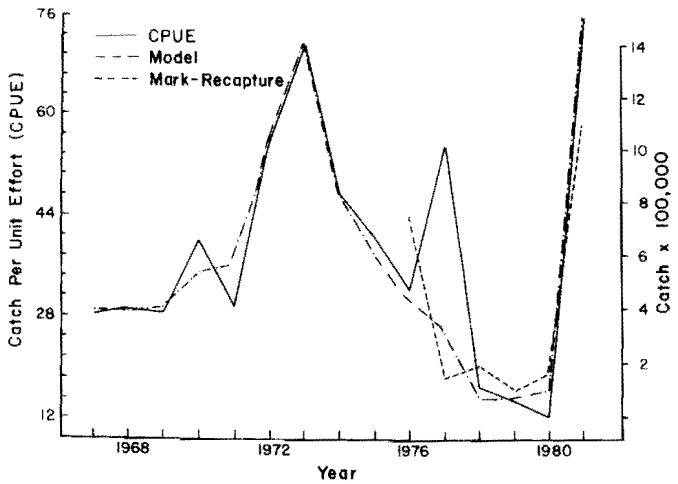

Figure 7. Population trends of Arctic cisco in the Colville River commercial fishery based on CPUE, model, and mark–recapture data. Source: Gallaway et al. (1983).

Barrow and the Colville River (McPhail 1966; Craig and Haldorson 1981). This species is not abundant in the study area and is often confused with the Arctic cisco because the two species look alike.

Marine Species

Relatively few marine fishes are harvested for several reasons: (1) marine species are generally small fish that yield relatively little meat for the effort expended, (2) some of the most common marine species (fourhorn sculpin, Arctic flounder) are not desired tablefare, and (3) the marine species that are eaten (Arctic cod, saffron cod) are too small to be caught by the principal fishing gear used (gill nets).

Arctic and saffron cod occur in marine waters throughout the study area. They are caught in winter by jigging a lure through the ice, but current fishing efforts are apparently fewer than occurred in the past.

Pacific herring are not abundant in the study area. Small populations occur along the northeastern Chukchi Sea coastline and near the Mackenzie River (Fig. 6). In the Point Lay area, herring are most abundant in August. Note that the term "herring" may also be used by fishermen to refer to least cisco and perhaps to other juvenile whitefish.

Relatively small numbers of capelin occur along the northeastern Chukchi Sea coast. These small fish are briefly abundant in the Point Lay area during the first week of August when they spawn along shorelines. Capelin are less abundant along the Beaufort Sea coastline, although large spawning runs occur occasionally. McAllister (1962) recorded such an event at Herschel Island during the last week of July 1960, but this has not been observed in recent years along the Beaufort coastline.

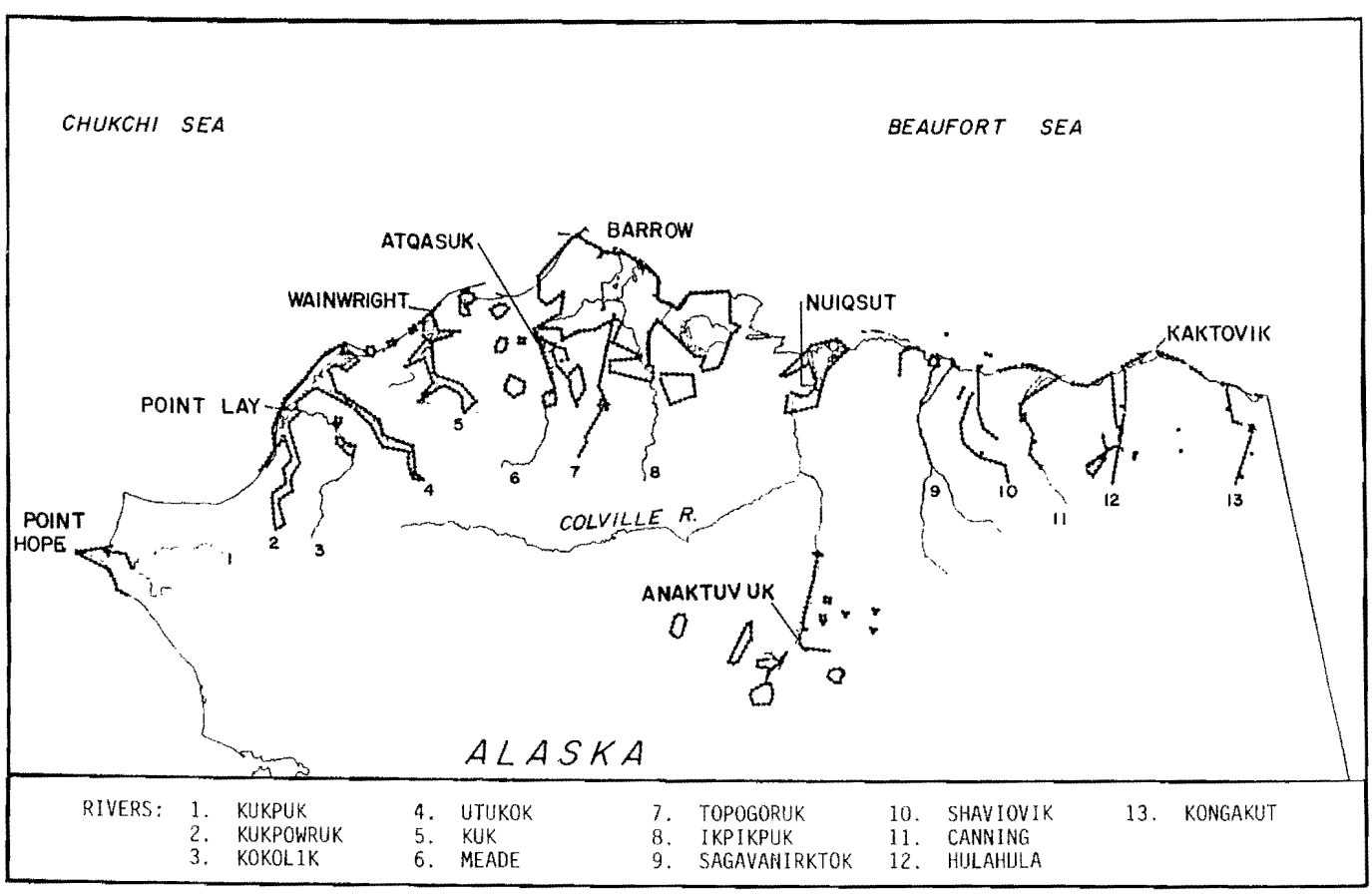

Figure 8. Regions used for subsistence fishing on the North Slope. Source: Pedersen (1979).

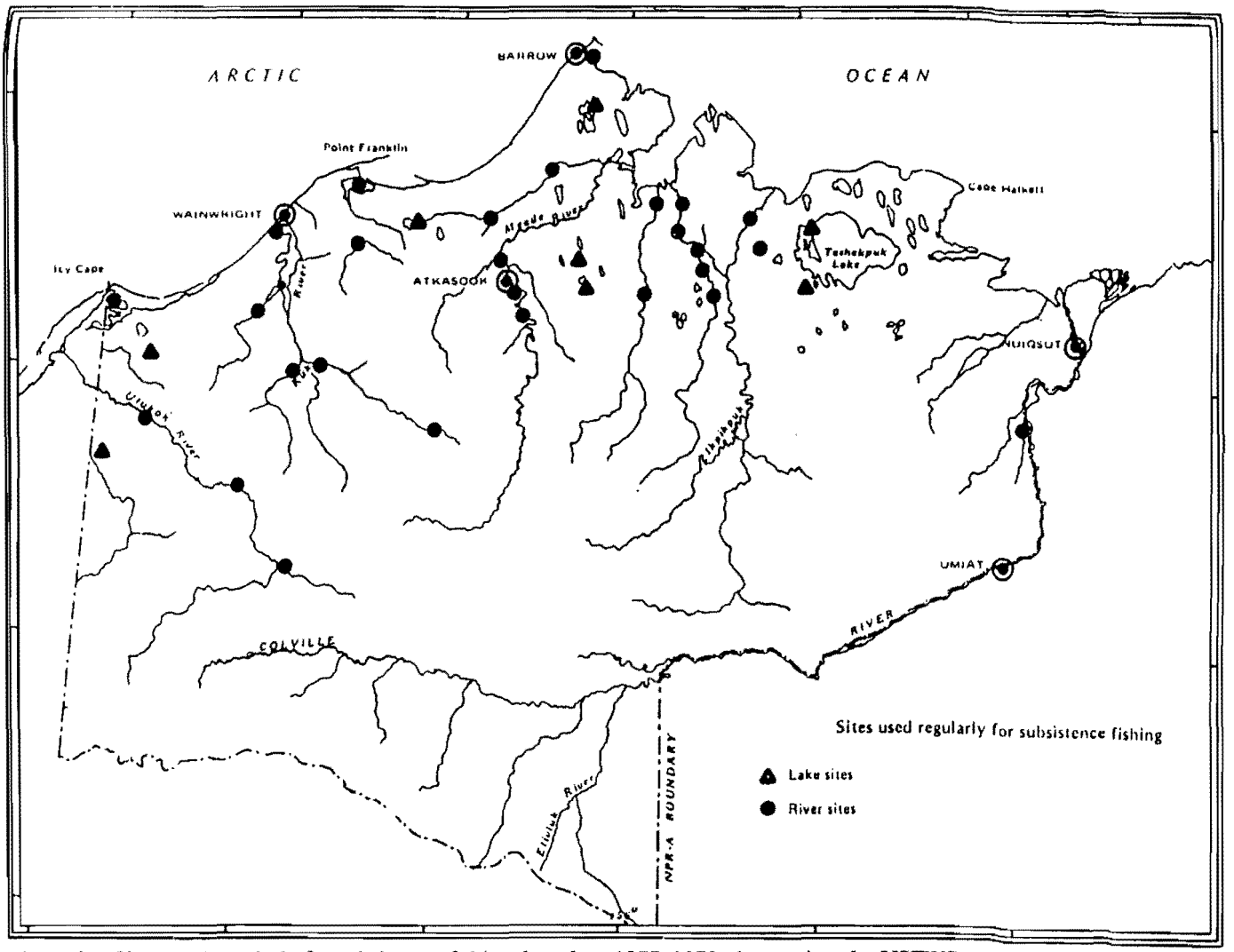

Figure 9. Sites used regularly for subsistence fishing, based on 1977–1978 observations by USFWS personnel and examination of the Land Use and Place Name Map of Arctic Alaska. Source: U.S. Department of the Interior (1978).

Fourhorn sculpin are often caught by subsistence fishermen, but these fish are an unwelcome catch because their sharp spines and "horns" are difficult to untangle from gill nets and because there is little edible reward for doing so. Some sculpins were eaten by villagers in the distant past, but today these fish are discarded.

Freshwater Species

The Arctic grayling is the principal freshwater fish caught on the North Slope. It is widely distributed and abundant in streams and lakes. Many are caught in subsistence fisheries in the Kukpowruk River by Point Lay fishermen and in the Meade River by Atqasuk fishermen; more are caught incidentally during other subsistence or recreational activities.

Burbot, lake trout, and other freshwater species are also caught, but less frequently than grayling.

SUBSISTENCE FISHERIES

Subsistence fishing in arctic Alaska occurs throughout the study area (Figs. 8 and 9). Most fishing occurs near the villages but some also occurs away from the villages at traditional fish camps.

Fishing consists primarily of gillnetting for anadromous fishes during the open-water season and also later in fall when gill nets can be safely set under the ice (Fig. 10); lesser numbers of fish are also caught by angling in summer and by jigging a lure through the ice in winter. Gill nets are usually set adjacent to shorelines because fish catches are generally highest there. A motorized skiff is used to reach most gill net sites, and nets are checked at about daily intervals. Fish caught are either cooked fresh or stored by freezing or drying. In modern times, most of the fish catch on the North Slope is for human consumption rather than for dog food.

As previously described, the species harvested differ

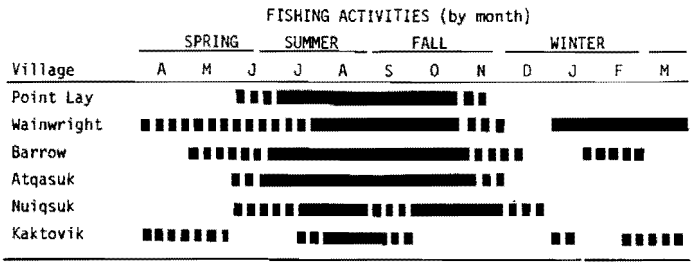

Figure 10. Seasonal patterns of fishing activities at North Slope villages. Solid lines indicate periods when harvests usually occur; broken bars indicate occasional fishing efforts. Sources: Compiled by ADFG (1986) from Schneider (no date), Ivie and Schneider (1979), Hoffman et al. (1978), Schneider et al. (1980), Nelson (1981), Jacobson and Wentworth (1982), and Galginaitis et al. (1984). The Nuiqsut pattern is based on George and Nageak (1986) and Moulton et al. (1986).

according to the location of each village (Table 2) and the uneven distributions of anadromous fishes in the study area (Fig. 4). In addition, freshwater fishes are taken in inland areas, and marine fishes are occasionally caught in coastal waters. Invertebrates are rarely collected in modern times.

The following sections summarize information about contemporary subsistence fisheries at each village. While a number of reports describe fishing activities, few provide quantitative estimates of annual fish harvests. Locations and years for which such quantitative data are available are as follows: Point Lay, 1983; Wainwright, 1973; Barrow, 1973; Atqasuk, 1983; Nuiqsut, 1985, 1986; and Kaktovik, 1973, 1975, 1985. Some partial estimates of harvests are also available for Barrow (1962, 1986), Nuiqsut (1984, 1985, 1986), and Kaktovik (1985).

Point Lay

The small village of Point Lay is located on the Chukchi Sea coast adjacent to Kasegaluk Lagoon. The village was formed by the consolidation of numerous settlements in the region in 1930 (Schneider and Bennett 1979). In 1985 the population size was 142 people.

Fishing activities at Point Lay have been described in two reports (Schneider and Bennett 1979; Craig and Schmidt 1985), which provide the basis for this section. Supplementary information is also provided in other reports (Craig and Schmidt 1982; Alaska Consultants et al. 1984; Braund and Burnham 1984).

Fishery Description

As with the other North Slope villages, the area encompassed by subsistence fishing at Point Lay is large, including coastal waters from Icy Cape to the southern end of Kasegaluk Lagoon, and inland waters including the Utukok, Kokolik, and Kukpowruk Rivers (Fig. 8). Summer and fall are the periods when most fishing occurs at Point Lay (Fig. 10).

Summer gill net fishing is conducted primarily in coastal waters in July and August. Coastal areas of primary and secondary importance are shown in Figure 11, but in recent years most fishing apparently has occurred within several miles of the village (Fig. 12), primarily on the lagoon side of the barrier islands. Some additional fishing occurs at Sitkok Point and at several permanent hunting camps located on both the barrier islands and the mainland south of Point Lay near Kukpowruk and Naokok passes. Summer fishing gear consists of monofilament or stranded nylon gill nets 100–150 feet in length and 6 feet deep with 3–5-inch stretched mesh. Species caught are pink salmon, chum salmon, and herring, with occasional char, whitefish, and cisco.

During fall, a grayling fishery occurs 10–15 miles upstream on the Kukpowruk River. This occurs around October, depending on freeze-up conditions, and may extend over several days or weeks and involve a relatively large number of villagers. Most grayling are caught by jigging a lure through holes drilled in the ice.

Harvest Quantity

Although fish have been described as a primary resource for the village and an integral part of their summer and fall subsistence activities (Schneider and Bennett 1979; Braund and Burnham 1984), the harvest was sparse during the only year (1983) when catches were monitored (Craig and Schmidt 1985).

In 1983 the summer fishery was brief (4–11 Aug.) and was directed toward the capture of salmon migrating past the village (Table 3). Only four fishermen participated, for a combined effort of approximately 16 man-days. Craig and Schmidt (1985) assessed the harvest at the village by inspection of daily catches or interviews with the fishermen after each catch, and this quantity was doubled to account for possible catches away from the village that were not observed. An estimate of the fall fishery was obtained by interviews with local residents.

The summer fishery (143 lb, mostly pink salmon) and fall fishery (250–300 lb, mostly grayling) yielded a total catch of about 400–450 pounds, for an annual per capita catch of 3–4 pounds in 1983. Residents suggested that the 1983 harvest was smaller than occurs in most years. The previously mentioned cycles in the abundance of pink salmon in arctic waters (i.e., pinks are less abundant in odd-numbered years) probably contributed to the low summer harvest in 1983.

Wainwright

Wainwright is a small community on the Chukchi Sea coastline adjacent to Wainwright Inlet (also called Kuk

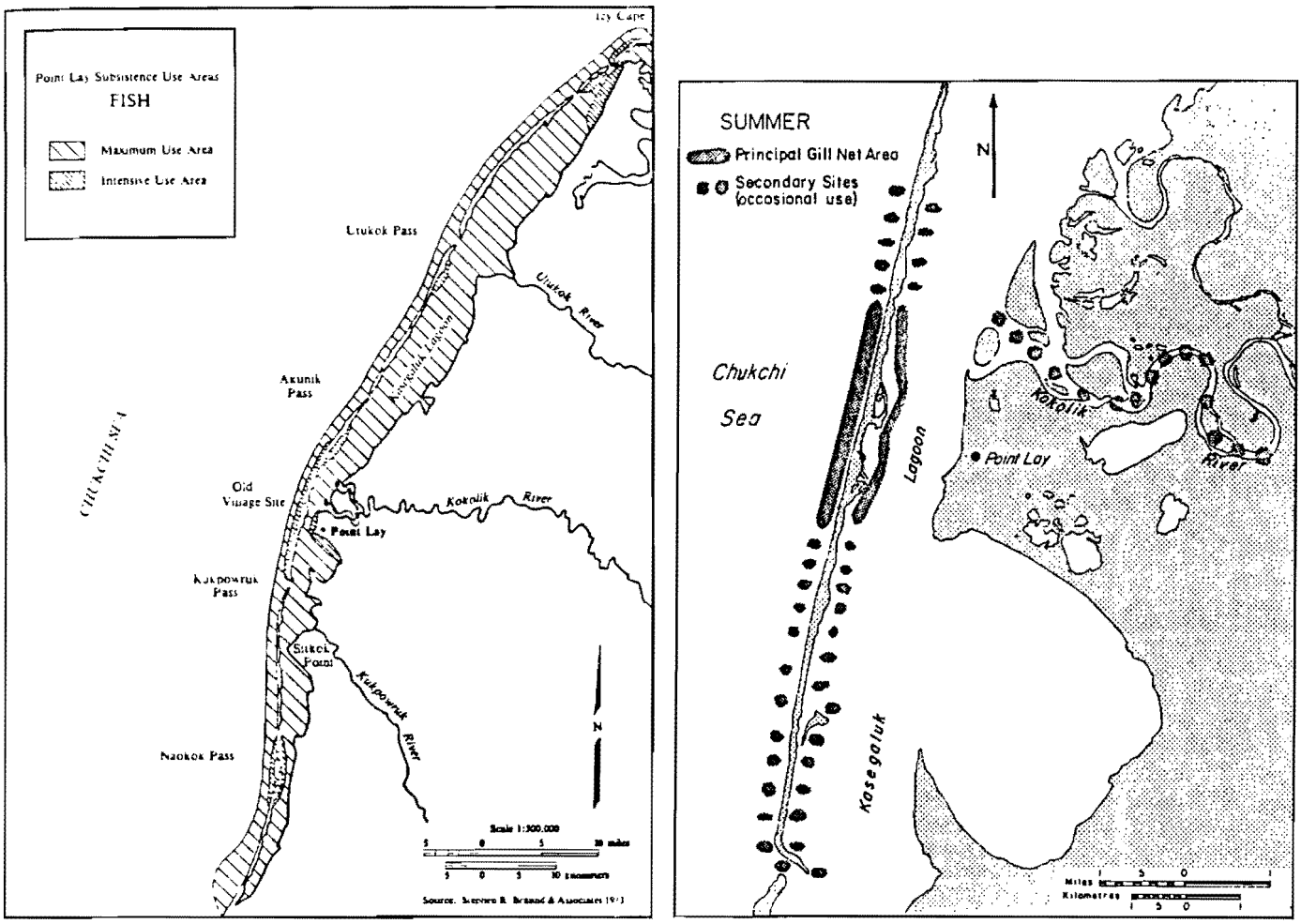

Figure 11. Point Lay subsistence use areas for coastal fishing. Source: Braund and Burnham (1984).

Figure 12. Point Lay fishing sites in 1983. Source: Craig and Schmidt (1985).

Lagoon or lower Kuk River). In 1985 the population size was 507.

The annual cycle of fishing activities at Wainwright has been described in detail by Nelson (1981) and the John Muir Institute (JMI 1983). Nelson based his description on research he carried out between 1964 and 1981. JMI conducted their household surveys in 1982. Supplementary information is also provided in several other reports (Bane 1966; Nelson 1966, 1969; Ivie and Schneider 1979; Craig and Schmidt 1982; Alaska Consultants et al. 1984; Braund and Burnham 1984).

Fishery Description

Fishing at Wainwright may occur year-round, but efforts are greatest in late summer and mid-winter (Fig. 10). The areas fished include nearshore coastal waters between Point Franklin and Icy Cape, and inland waters primarily along the Kuk River but also on the Kugrua, Utukok, and other nearby rivers (Figs. 8 and 13).

In summer (July and Aug.), people fish with gill nets along the beach in front of the village or in Wainwright Inlet (Fig. 14). Ocean gill nets, set about 50 m from shore, have 3–6-inch stretched mesh; river gill nets have slightly smaller meshes (3–5 in). JMI (1983) noted that a typical ocean catch in late June was 10–18 fish per day, mostly pink and chum salmon with a few char and other species. Nets set in late July also caught mostly pink and chum salmon (Craig and Schmidt 1982). Fishing in the inlet yields rainbow smelt, whitefish, cisco, and cod.

In late summer and fall (Aug.–Oct.), fishing in the Kuk River intensifies. Nelson (1981) observed fish camps at several upstream locations in the Kuk drainage (see also Fig. 9) where grayling, cisco, burbot, and smelt were taken.

In winter (Jan.–Mar.), rainbow smelt are caught in Wainwright Inlet by jigging with a slender pole about 2.5 feet long with 4–6 feet of monofilament line and a small bright hook attached (Nelson 1981). The smelt from the inlet are highly regarded and may be exchanged between villages. JMI (1983) noted that these smelt have the dis-

Table 3. Estimated total subsistence harvest of fishes in the Point Lay area, 1983 (source: Craig and Schmidt 1985).

	Estimated number of fish caught			
	Point Lay	Other sites*	Total	Estimated total weight (lb)†
Summer fishery				
Pink salmon	18	N	36	86
Herring	30	N	60	21
King salmon	1	N	2	12
Arctic char	3	N	6	12
Bering cisco	5	N	10	11
Rainbow smelt	3	N	6	1
Totals	60		120	143
Fall fishery				
Grayling	N	N	N	250–300‡

* N (not monitored). Sites away from Point Lay such as hunting camps were not monitored. Observations suggest that the harvest of fish on such occasions was very low, if any, during the 1983 summer. Therefore, it was conservatively assumed that the harvest away from the village was similar to that at the village.

† Original data of Craig and Schmidt (1985) have been corrected here. Total weight = number of fish × average weight of each species. Average weights were estimated from specimens caught during the study.

‡ Total weight was estimated by local fishermen.

tinction of being the only species of animal or plant that is regularly bought and sold in Wainwright.

Smelt are the only important fish regularly harvested in winter. Tom-cod (saffron cod) in the ocean were formerly caught in winter but they are not fished at present.

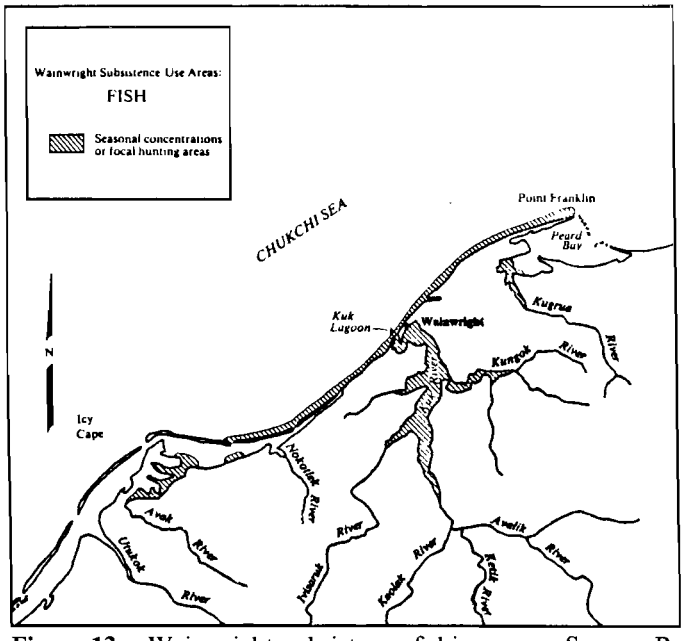

Figure 13. Wainwright subsistence fishing areas. Source: R. Nelson (1981), North Slope Borough as presented in Braund and Burnham (1984).

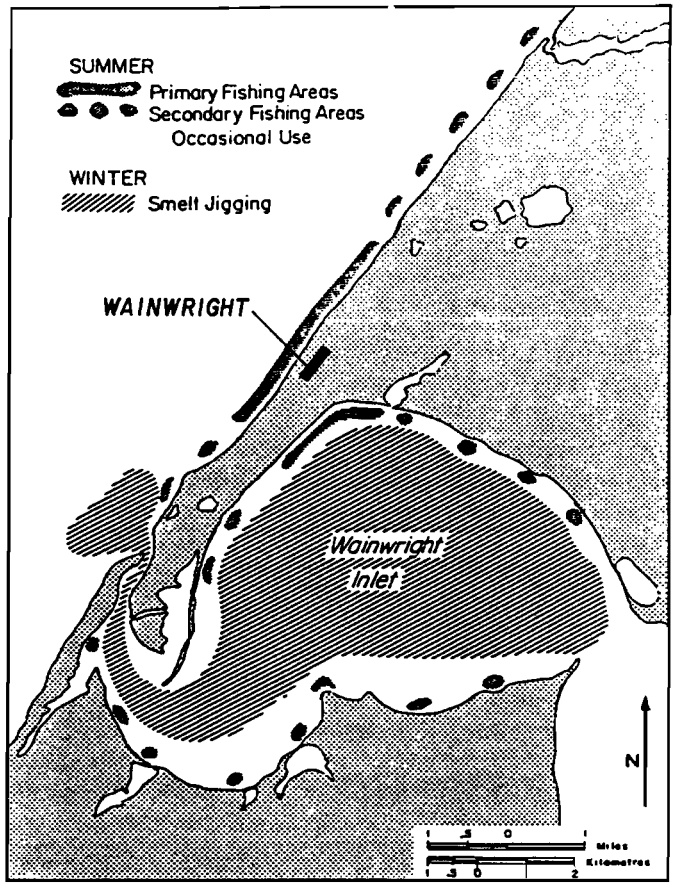

Figure 14. Wainwright subsistence fishing areas. Source: Craig and Schmidt (1982).

Harvest Quantity

The only quantitative estimate of fish harvests at Wainwright is provided by Patterson (1974), who based his estimate on information supplied by village representatives from 1969 to 1973. Harvest estimates found in several later reports all stem from Patterson's data (Patterson and Wentworth 1977; AEIDC 1978; Stoker 1983; ADFG 1986).

During 1969–1973, the average annual fish harvest was low (about 3,800 lb), amounting to less than 1 percent by weight of the total harvest of all resources (mammals, birds, fish, plants) during the same period (Table 4). The annual per capita catch of fish was 9 pounds. Stoker (1983) used Patterson's figures as the estimated average fish catch over the 20-year period 1962–1982. The Alaska Department of Fish and Game (ADFG 1986) cautions that these quantities are rough approximations because data were not systematically collected or verified.

Nelson (1981) observed that there has been a resurgence of interest in fishing at Wainwright in recent years. In 1976, for example, the North Slope Borough (cited in AEIDC 1978) estimated that a typical subsistence harvest of fish was 500 pounds for a six-member family, which equals an annual per capita consumption of 83 pounds. Supportive documentation for the derivation of this es-

Table 4. Estimated harvest of fish at Barrow, Wainwright, and Kaktovik based on interviews with village representatives, 1969–1973 (source: Patterson 1974).

	Fish harvests					
	Barrow		Wainwright		Kaktovik	
Fish	Number	Weight (lb)	Number	Weight (lb)	Number	Weight (lb)
Herring	10,000	—	—	—	—	—
Whitefish (large)	8,000	—	—	—	—	—
Whitefish (small)	8,000	—	600	—	2,500	—
Grayling	2,500	—	150	—	—	—
Coho/silver salmon*	200	—	—	—	—	—
Pink salmon	200	—	50	—	—	—
King salmon*	200	—	30	—	—	—
Smelt	—	—	—	1,000	—	1,000
Trout	50	—	200	—	1,000	—
Arctic char	100	—	—	—	2,500	—
Burbot	100	—	—	—	—	—
Tom cod	500	—	—	—	—	—
Totals						
Number	29,850		1,030+		6,000+	
Weight (dressed lb)		61,550		2,840		15,500
Weight (total lb)†		83,000		3,800		21,000
% Fish in total harvest‡		5		0.6		14
Per capita consumption (lb)		32		9		131

* Coho and king salmon are rare in these waters (see Craig and Haldorson 1985). These fish could have been sea-run chum salmon.

† Calculated as dressed weight = 75% total weight.

‡ Includes mammals, birds, fish, and other wildlife.

timate was not provided in the Arctic Environment Information and Data Center (1978) report.

Barrow

Barrow is the largest community on the North Slope (excluding the industrial center in the Prudhoe Bay area). The present-day site of Barrow has probably been occupied continuously for about 1,300 years. The population has grown steadily in recent years to 3,075 people in 1985, which includes a large proportion of non-natives (40%).

Descriptions of contemporary fishing activities at Barrow have been made by several authors (Pedersen et al. 1979; Schneider et al. 1980; Braund and Burnham 1984). Supplementary information, particularly of earlier fishing practices, is also available (e.g., Murdoch 1884; Sonnenfeld 1956; Wilimovsky 1956; Hall 1983; Stern 1985). It should also be noted that subsistence fishing activities by Barrow residents overlap spatially with those of Atqasuk residents (Fig. 3), but the degree to which this currently occurs is not known.

Fishery Description

Fishing by Barrow residents occurs primarily in summer and fall (Fig. 10). The area fished is extensive (Fig. 15) because hunters traveling from Barrow often supplement their food supply with fish. In addition, numerous fish camps are situated on lakes and rivers in the region.

Coastal fishing areas extend from Peard Bay to Pitt Point (Fig. 15), but most fishing occurs closer to Barrow in three areas: (1) along the Chukchi Sea coastline from Point Barrow to Walikpa ("Ualiqpaat") Bay located 14 miles SW of Barrow, (2) inside Elson Lagoon near Barrow, and (3) along the barrier islands of Elson Lagoon. Fish are usually caught along shorelines by monofilament gill nets up to 50 feet long with 3.5-inch mesh. Species taken are salmon, whitefish, cisco, and char. Summer collections of shore-spawning capelin and winter jigging for Arctic cod are activities that have diminished in recent years.

While coastal fishing can be an important source of fish, most of the harvest occurs at inland fish camps, particularly in lakes and rivers that flow into the southern end of Dease Inlet. As summer progresses, inland fishing activities increase and continue into November. Some families spend the summer and fall at fish camps in the Inaru, Meade, Topogoruk, and Chipp drainages. Fish are caught mostly by gill net, with some angling. Species harvested include whitefishes, least cisco, grayling, and a few burbot and salmon.

Harvest Quantity

Harvest data for Barrow include an annual catch estimate for the period 1969–1973 (Patterson 1974), and partial catches for 1962 (Hanson et al. 1966) and 1986

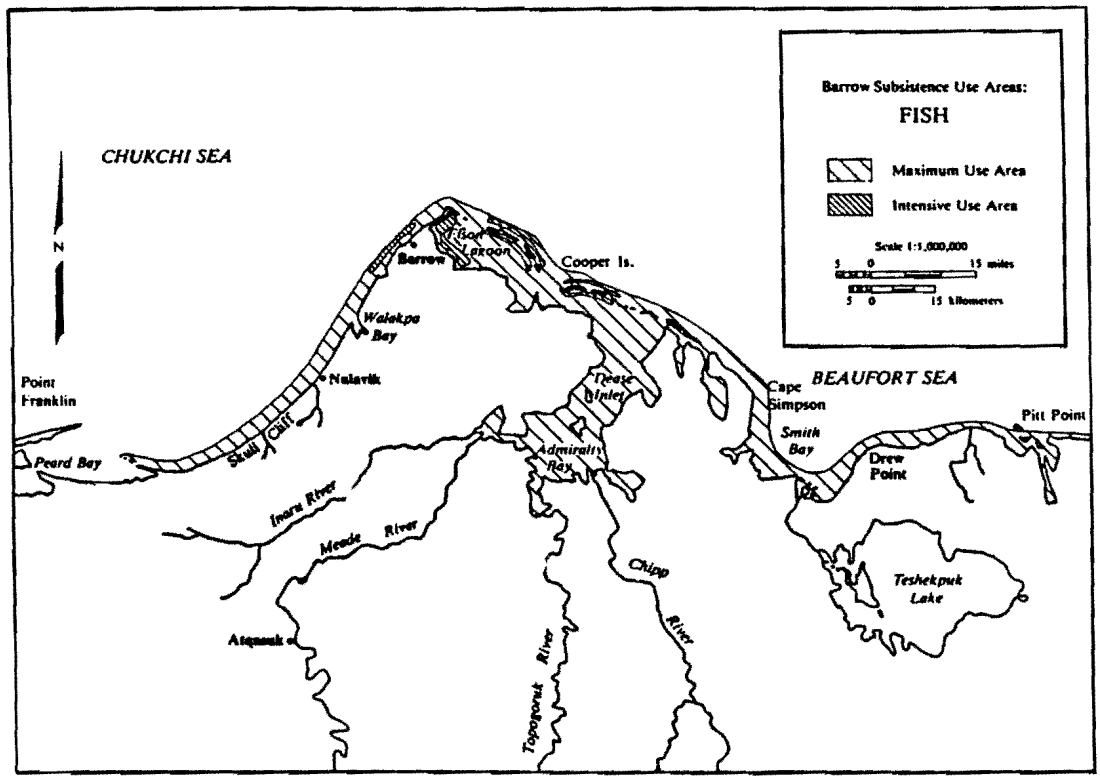

Figure 15. Barrow subsistence fishing areas. Source: Braund and Burnham (1984).

(George 1986). Estimates found in several other reports all use Patterson's data (Nielson 1977; Patterson and Wentworth 1977; AEIDC 1978; Hall 1983; Stoker 1983; ADFG 1986).

During 1969–1973, the average annual harvest of fish was about 83,000 pounds (Table 4). This amounted to 5 percent by weight of the total harvest of subsistence resources and an annual per capita catch of 32 pounds of fish. Stoker (1983) used Patterson's figures as the estimated annual harvest over the 20-year period 1962–1982. Limitations concerning this quantification of the fish harvest were mentioned earlier. Also, the smelt listed in the "Barrow harvest" (Table 4) are actually fish that were caught in Wainwright Inlet and purchased by Barrow residents (Charlie Brower, pers. comm.).

The 1962 partial estimate of fish harvests was derived from interviews with 248 adults at Barrow (Hanson et al. 1966). Fish (mostly whitefish) accounted for 23 percent by weight of the total subsistence resources consumed by adults and 7 percent of an adult's total diet of both subsistence and store foods. Fish consumption was estimated to be 2.0–2.2 pounds per week, for a yearly per capita consumption of 104 pounds per adult. (An extrapolation of this information to calculate the total annual harvest would require more information than is available, i.e., the number of both adults and nonadults present in 1966, the amount of fish consumed by nonadults, and the amount of fish used for other purposes such as dog food.)

The 1986 partial estimate of fish harvests was for the fall fishery in the lower Inaru River. During 17–19 October 1986, George (1986) monitored the catch at "Pulayaq" located 2 miles west of Sisgravik Lake. Fishermen used gill nets 50–60 feet long with 2.5–3.0-inch mesh. The observed catch per unit effort was 93 fish per 24-hour set, and consisted of 424 fish equaling about 675 pounds (using the average weights listed in Table 1). The catch composition was least cisco (45%), broad whitefish (36%), humpback whitefish (16%), Arctic cisco (1%), fourhorn sculpin (1%), and burbot (0.5%).

Atqasuk

In the mid-1970s, the village of Atqasuk was reestablished on the Meade River 60 miles south of Barrow. The population had grown to 248 people in 1985. As previously noted, the subsistence activities of Atqasuk residents overlap spatially with those of Barrow residents (Fig. 3), but the degree to which this currently occurs is not known.

The most detailed description of the Atqasuk fishery is provided by Sekerak et al. (1985). Additional information (Pedersen et al. 1979; Schneider et al. 1980) and supplementary notes (Craig and Schmidt 1982; Hall 1983; Braund and Burnham 1984; ADFG 1986) are also available.

Fishery Description

Most subsistence fishing by Atqasuk residents occurs in summer and fall (Fig. 10) in the Meade River within

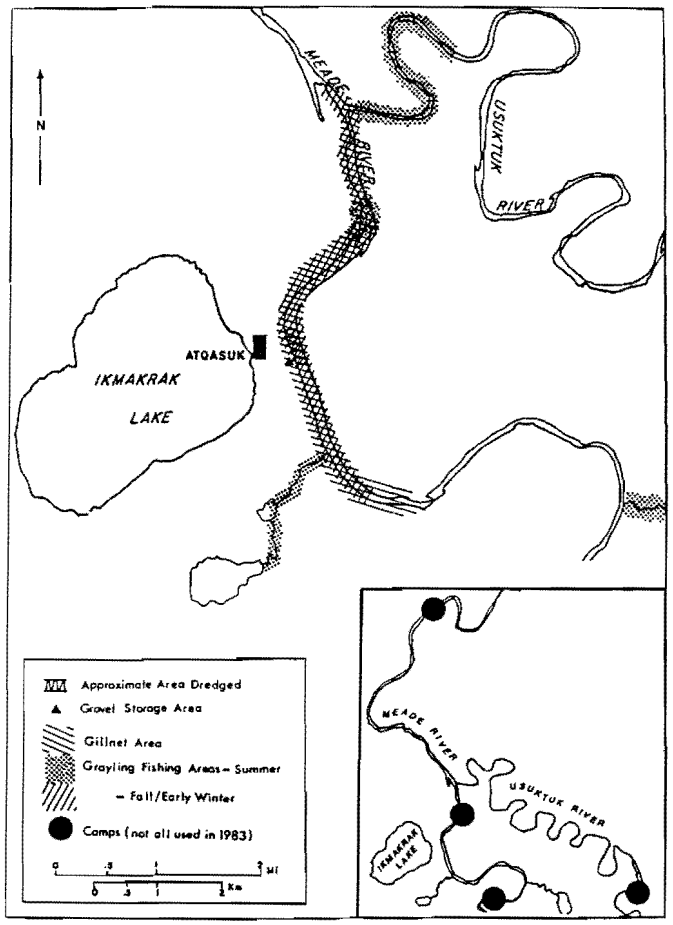

Figure 16. Important fishing areas adjacent to Atqasuk, 1983. Source: Sekerak et al. (1985).

a few miles of the village (Fig. 16). Fish camps are also located on two nearby streams (Usuktuk and Nigisakituvik Rivers) and farther downstream on the Meade River near the Okpiksak River.

Gill nets (usually 50 ft long with 2.5–5.5-in stretched mesh) are the main gear used, although angling and some use of set lines (for burbot) also occurs. Fishing in the Meade River begins after the spring freshet in mid- to late June when debris in the water has decreased. Fishing declines in September when drifting ice prohibits use of gill nets. Fall and early winter fishing (gill nets and jigging) begin after freeze-up and extend through late November or early December.

Humpback whitefish and least cisco accounted for 96 percent of the summer catch in 1983. Other species caught were grayling, broad whitefish, burbot, and in some years chum salmon. Winter catches in the Meade River near the village consisted mostly of humpback whitefish, grayling, and some broad whitefish.

Harvest Quantity

Quantitative data are available only for 1983 when Sekerak et al. (1985) documented the fish harvest by means

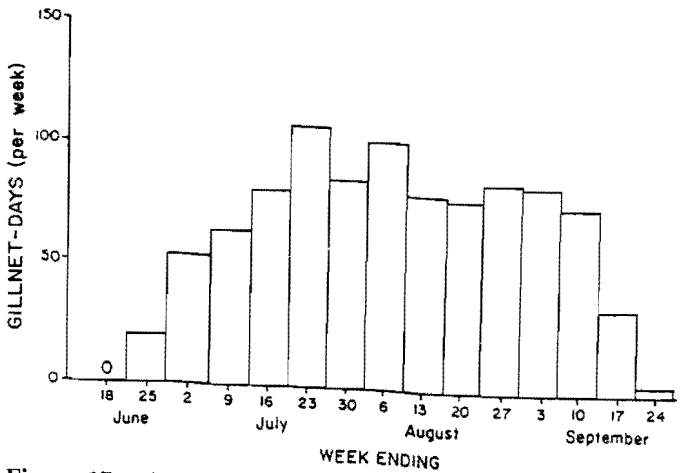

Figure 17. Atqasuk fishing effort during the summer gill net fishery in the Meade and Usuktuk Rivers, 1983. Source: Sekerak et al. (1985).

of direct observation, interviews, and questionnaires given to the fishermen.

In 1983, fishing effort was fairly constant from mid-July to early September when up to 12–16 gill nets were often in daily use, with an average effort of about 75 net-days per week (Fig. 17). The summer gill net fishery in the Meade and Usuktuk Rivers caught approximately 8,450 pounds of fish (Table 5). With the addition of summer catches by other gear (1,100 lb primarily by angling) and winter catches (2,700 lb), the total harvest was approximately 12,250 pounds. The annual per capita catch of fish was thus about 43 pounds in 1983 (when the population size was 231).

Table 5. Estimated fish harvest at Atqasuk in 1983 (source: Sekerak et al. 1985).

Fishery component	Estimated fish harvest	
	Number	Weight (lb)
A. Summer fishery (gill net)		
Humpback whitefish	3,285	4,380
Least cisco	4,283	3,730
Broad whitefish	114	174
Burbot	157	135
Grayling	43	31
Salmon*	—	—
Total	7,882	8,450
B. Summer fishery (angling, set line)		
All species	—	1,100
C. Winter fishery (gill net)		
All species	2,700	2,700†
Total	—	12,250

* Salmon are caught in some years (Craig and Schmidt 1982).
† Author's original estimate of 500 lb was derived from gill nets with smaller mesh size than is used in the fishery (A. Sekerak, pers. comm.), therefore average weights of whitefish and cisco from the summer fishery were substituted here.

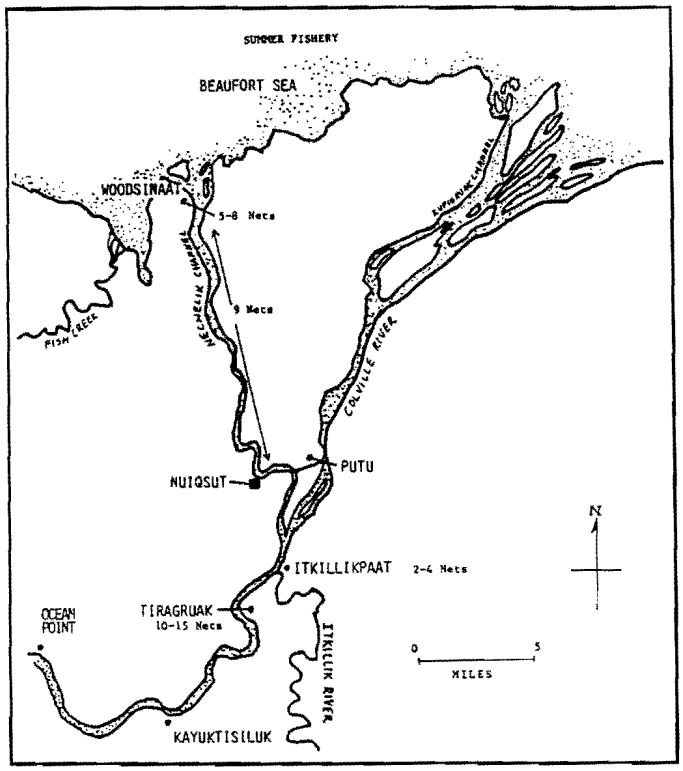

Figure 18. Nuiqsut summer fishery showing locations of gill nets in the Colville River delta, July 1984. Source: George and Nageak (1986).

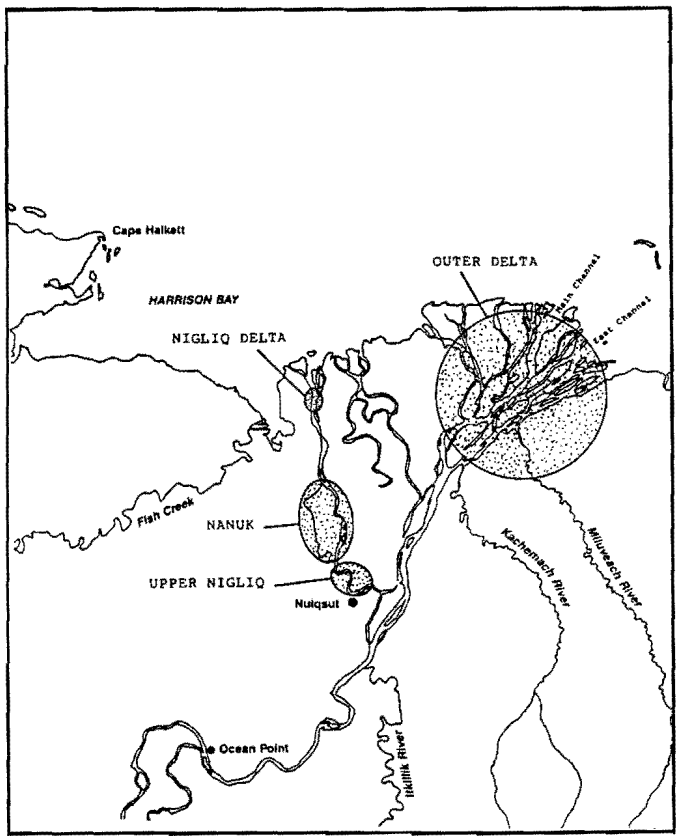

Figure 19. Nuiqsut under-ice fishing areas in fall and early winter. Source: Entrix (1987).

Nuiqsut

In 1973 the village of Nuiqsut was reestablished in the delta of the Colville River, and by 1985 the population size was 332 people.

The Colville River is well known for its abundance of fish (see also Fig. 4). The Colville Delta supports both a sizable subsistence fishery for Nuiqsut residents as well as the only commercial fishery (Helmericks) in the study area. The Nuiqsut fishery has received considerable attention in recent years, and several reports provide detailed information (Hoffman et al. 1978; Libbey et al. 1979; George and Kovalsky 1986; George and Nageak 1986; Moulton et al. 1986; Entrix, Inc. 1987). An additional report by Pedersen and Shishido (1988) was not available in time for this review. Supplementary information is available in several other reports (NSB 1979b; Craig and Schmidt 1982; Galginaitis et al. 1984; ADFG 1986).

Fishery Description

The fishery at Nuiqsut consists primarily of gill netting for anadromous fishes in the main channels of the lower Colville River and in nearby Fish Creek (Figs. 8, 18, and 19). Recent studies indicate that the main fishing periods occur in summer and fall/winter (Fig. 10) rather than spring and fall as indicated in earlier reports (e.g., Libbey et al. 1979).

Broad whitefish are the primary target of a gill net fishery in summer (June–Sept.). Fishing efforts are concentrated in three areas: the Nigliq (Nechelik) Channel, Fish Creek, and the Colville River upstream of Nuiqsut in the Tiragruaq area (Fig. 18). Large-mesh gill nets (50–100 ft long, 4–5.5-in stretched mesh) catch large specimens of broad whitefish and other species (Table 6). Daily catch rates are generally low at this time of year—two to five fish per net-day in July 1984 (George and Nageak 1986), and similar rates in 1985 (Table 6).

The fall/winter fishery is an under-ice effort primarily for Arctic cisco. Fishing efforts are concentrated in three areas: the upper Nigliq Channel near Nuiqsut, the lower Nigliq Channel near Woods Camp, and the outer Colville Delta on the main (Kupigruak) channel (Fig. 19). Additional fishing sites include the Fish Creek area and the Colville River upstream of the village near Kayuktisiluk (see Fig. 20).

Fall fishing begins in early October when the ice is safe to travel on, and extends into November. Peak fishing effort occurs during the last half of October. Sinking gill nets of 2.5–3.5-inch stretched mesh are the standard gear, with 3-inch mesh the most common. The catch rate is often about 15–32 fish per net-day and up to about 100 fish per net-day, which is considerably higher than the

Table 6. Nuiqsut summer fishery: fish sizes and catch per unit effort (CPUE) in large-mesh gill nets in 1985 (source: Moulton et al. 1986).

Species	Fork length (mm)		CPUE (fish/ net-day)
	Mean	Range	
Broad whitefish	529	365–650	1–8
Humpback whitefish	439	405–525	0–1
Arctic char	600	520–765	0–4
Pink salmon	524	475–595	—

catch rate during the summer fishery. While Arctic cisco are the target of this fishery, large numbers of least cisco are caught as well as some humpback whitefish, broad whitefish, rainbow smelt, and fourhorn sculpin. The abundance of Arctic cisco in the Colville Delta is highly variable, as previously described (Fig. 7).

Harvest Quantity

Harvest data for Nuiqsut include annual catch estimates for 1985 (Moulton et al. 1986) and 1985–1986 (Pedersen and Shishido 1988), and partial catch estimates for 1984 (George and Nageak 1986), 1985 (George and Kovalsky 1986), and 1986 (Entrix, Inc. 1987).

Moulton et al. (1986) and Pedersen and Shishido (1988) used different methods but arrived at similar estimates for the 1985 fish harvest at Nuiqsut. Moulton et al. (1986) estimated the harvest by interviews with local fishermen, periodic counts of nets in the water, and occasional trips with the fishermen as they tended their nets. About 20 groups of fishermen participated in the summer fishery.

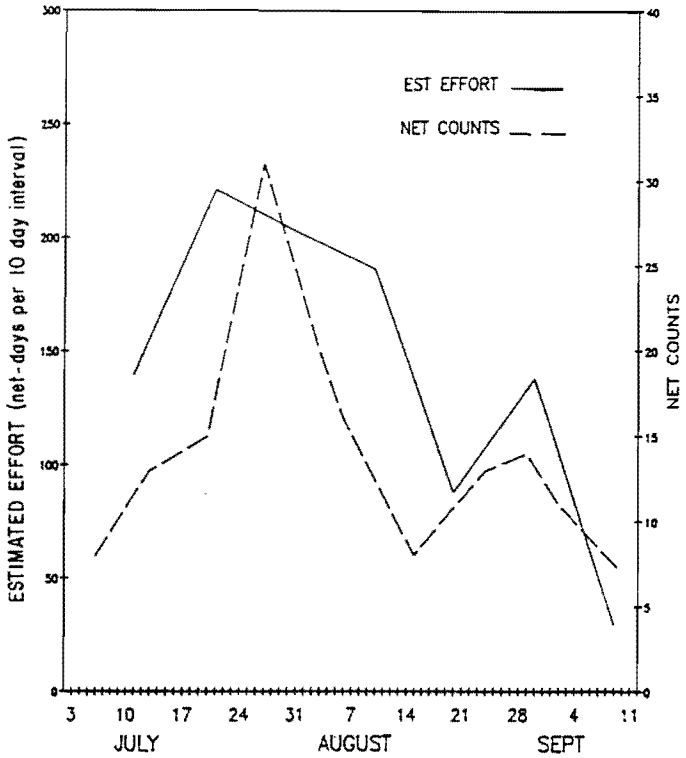

Figure 20. Nuiqsut summer fishery as seasonal gill net effort, 1985. Source: Moulton et al. (1986).

Fishing effort was greatest in late July and early August (Fig. 20), with a total effort of about 1,000 net-days. The summer catch totaled about 19,260 pounds, mostly broad whitefish (Table 7). In fall, approximately 30 fishing groups had a combined effort of about 1,800 net-days (not including 910 net-days by the commercial fishery) and

Table 7. Nuiqsut fish harvest in 1985 (source: Moulton et al. 1986).

Season and location	Number harvested*						Total (lb)
	Broad whitefish	Humpback whitefish	Arctic char	Arctic cisco	Least cisco	Other	
A. Summer fishery							
Nigliq Channel	3,053	293	126				
Colville River	596	9	189				
Fish Creek	180						
Total number	3,829	302	315			—	
Total weight (lb)*	17,230	580	950			500†	19,260
B. Fall fishery							
Nigliq Channel (upper)	1,468			17,878	1,871		
Nigliq Channel (lower)				8,500			
Colville Delta (outer)				20,303	13,943		
Total number	1,468			46,681	15,814		
Total weight (lb)*	6,610			43,120	11,170		60,900
Total weight (lb), summer and fall fisheries							80,160

* Does not include Helmericks' commercial catch.

† Estimated based on catch proportion (other species = 4% of catch).

Table 8. Nuiqsut fish catch based on preliminary data from household surveys, 1985–1986 (source: Pedersen and Shishido 1988).

Fish	Estimated usable weight (lb)		Estimated total harvest†		
	Subsample*	Total	No. fish caught‡	Weight/fish (lb)§	Total weight (lb)
Broad whitefish	14,137	26,674	7,845	4.5	35,300
Arctic cisco	11,509	21,715	31,021	0.9	27,920
Least cisco	3,940	7,366	14,732	0.7	10,310
Grayling	1,920	3,587	3,986	1.0	3,990
Humpback whitefish	1,830	3,453	4,316	1.9	8,200
Arctic char	1,562	2,947	1,053	3.0	3,160
Burbot	1,208	2,279	570	4.0	2,280
Salmon	719	1,357	438	5.0	1,750
Smelt	84	158	3,160	0.2	630
Lake trout	48	91	23	8.5	200
Round whitefish	5	9	9	0.7	6
Totals	36,962	69,636	67,153		93,746

* Of the 75 households in the village, 40 (53%) were sampled.

† Pedersen (1987) estimated the number of fish harvested and then converted this to the edible or usable weight of the fish. Because the ratio of usable weight:total weight was not listed, it was necessary to recalculate the number of fish caught and then multiply by total fish weights to determine the total weight of the total harvest.

‡ Derived from Pedersen's conversion factors.

§ Derived from Colville Delta data (Moulton et al. 1986) where possible; otherwise from Table 1.

caught about 60,900 pounds. Some grayling and other freshwater fishes were also caught, but the quantity is thought to be small compared to the documented portion of the harvest. The annual catch was thus about 80,160 pounds, for an annual per capita catch of 241 pounds. It should be noted, however, that some of this catch is not consumed locally but is shipped to Barrow.

Pedersen and Shishido's (1988) report provided a preliminary estimate of the fish harvest at Nuiqsut for the period July 1985 to June 1986. Because relatively little fishing occurs from January to June at the village (Fig. 10), these authors' data pertain mostly to 1985. Based on interviews with 40 of the 75 households in the village, they estimated the fish harvest of this subsample to be about 37,000 pounds of usable or dressed weight (Table 8). An expansion of these data to all 75 households in the village yields 70,000 pounds dressed weight or 94,000 pounds total weight. The annual per capita catch was thus about 282 pounds of fish, although as mentioned above, some of this catch was shipped outside the village. (For comparative purposes, the 1985 commercial fishery in the Colville Delta harvested approximately 20,600 lb of Arctic cisco and 12,300 lb of least cisco.)

Three partial estimates of fish harvests at Nuiqsut are as follows:

(a) 1984. Based on limited data, George and Nageak (1986) estimated that the summer fishery caught more than 1,000 broad whitefish, and the fall fishery caught about 12,000 Arctic cisco and probably the same number of least cisco.

(b) 1985. Data collected by George and Kovalsky (1986) were used by Moulton et al. (1986) to arrive at the total 1985 estimate described above.

(c) 1986. In a detailed study of the fall fishery, Entrix, Inc. (1987) documented that 33,522 Arctic cisco and 6,805 least cisco were taken in the subsistence fishery. This amounts to about 35,700 pounds of fish (calculated using the conversion factors of Moulton et al. [1986]). Due to a reduced fishing effort in 1986 at Nuiqsut, the fall harvest was only 59 percent of that taken the previous year (60,900 lb).

Kaktovik

The village of Kaktovik is located on Barter Island adjacent to the Arctic National Wildlife Refuge. In 1985 the population size was 220.

Several descriptions of fishing activities at Kaktovik are available (Griffiths et al. 1977; Wentworth 1979; Jacobson and Wentworth 1982; Envirosphere 1986) and supplementary information is found in other reports (Furniss 1974, 1975; USFWS 1982; Craig and Schmidt 1982; Pedersen et al. 1985; Stern 1985; ADFG 1986). In addition, the United States Fish and Wildlife Service and ADFG conducted household surveys to determine patterns of resource use in 1985–1986, but their report was not available in time for inclusion here, except for a summary table of fish catches which was provided by S. Pedersen (pers. comm.).

Fishery Description

While some fishing may occur year-round at Kaktovik, efforts are greatest during summer months (Fig. 10). Areas currently or formerly fished are widespread, extending along the coast from Prudhoe Bay to Demarcation Bay and far inland on many of the larger North Slope rivers (Figs. 8 and 21). These figures depict the extent of land

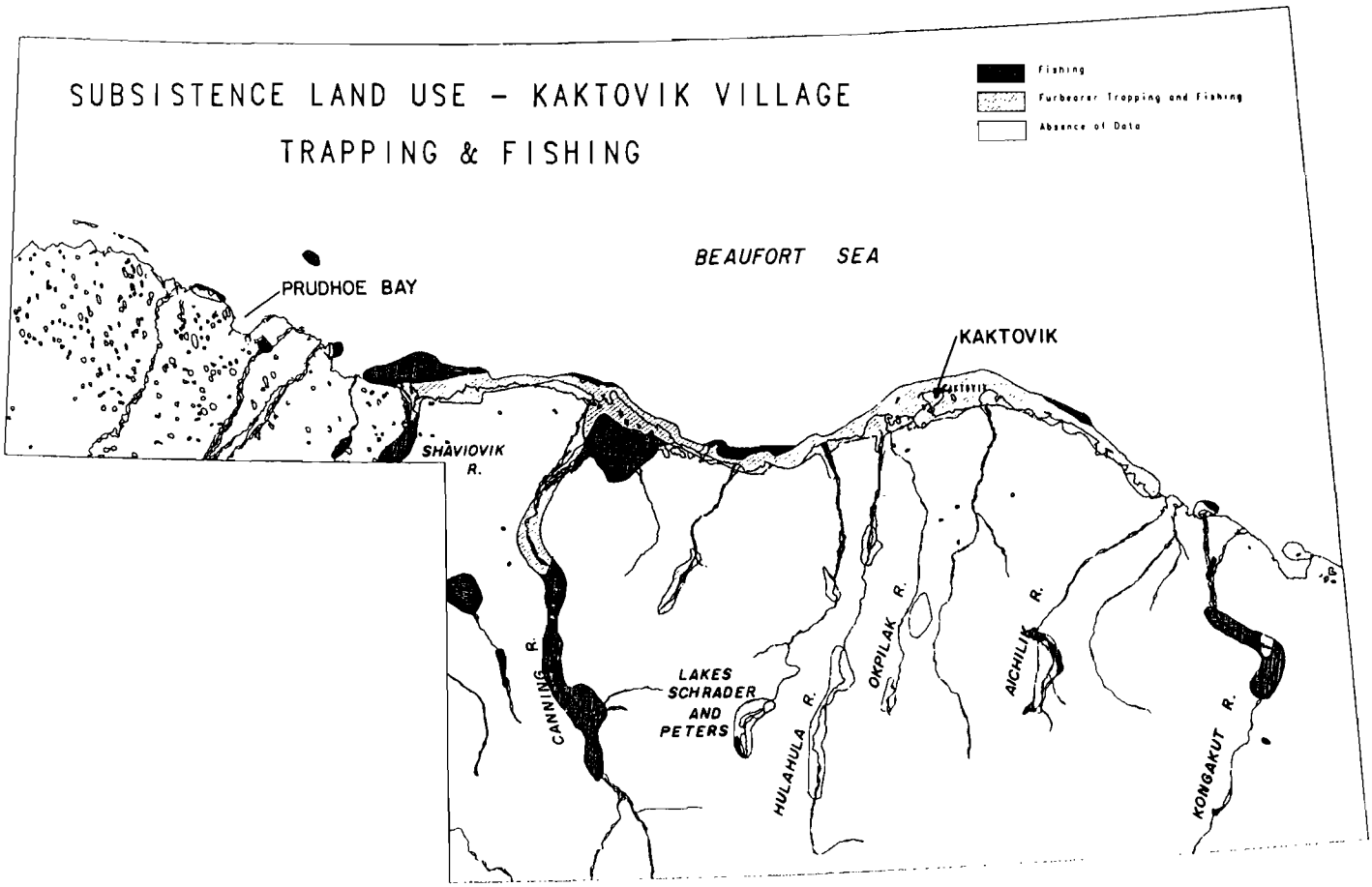

Figure 21. Kaktovik subsistence use areas for fish. Source: North Slope Borough, Geographic Information System, Anchorage, Alaska.

use by Kaktovik residents over the 60-year period from about 1923 to 1983 (Pedersen et al. 1985). In recent years, most fishing occurs in the vicinity of Barter Island (Fig. 22), at several fish camps along the coastline (e.g., Griffin Point), and in the Hulahula River (Griffiths et al. 1977).

The summer fishery is primarily a coastal gill net effort for Arctic char (early in the season) and Arctic cisco (later in the season). Fishing occurs around Barter Island, Bernard Spit, and Arey Island during the open-water season (June–Sept.) with peak fishing in July and August.

Gill nets are typically 100 feet long with 5-inch stretched mesh and are set several feet out from the edge of the shoreline. Some angling also occurs throughout the summer. Average sizes of fish caught in the 1985 summer fishery were 19 inches (482 mm) for Arctic char and 15 inches (387 mm) for Arctic cisco (Envirosphere 1986). As mentioned earlier in this report, tagging studies have shown that the char caught at Kaktovik can originate from North Slope streams between the Sagavanirktok and Firth Rivers, and that the Arctic cisco are caught during their migrations to or from the Mackenzie River.

Fishing activities are reduced in winter but occur in three general areas. First, the main effort is in the Hulahula River where char are caught at three spawning and overwintering sites (Fig. 21). Prior to freeze-up (Fig. 21), these fish are caught by seine or angling, and after freeze-up the fish are hooked by jigging lures through holes drilled in the ice. Second, lake trout are caught by jigging in Lake Schrader ("Neruokpuk Lake") in the headwaters of the Sadlerochit drainage. Some of these fish are up to 3 feet in length and weigh 20 pounds, but more typical weights are 4–5 pounds. Third, in some winters Arctic cod are caught by jigging in coastal waters near the village.

Harvest Quantity

Harvest data for Kaktovik include annual catch estimates for 1973 (Patterson 1974), 1975 (Griffiths et al. 1977), 1985 (S. Pedersen, pers. comm.), and a partial estimate for 1985 (Envirosphere 1986). Estimates found in several other reports all use Patterson's data (Nielson 1977; Patterson and Wentworth 1977; AEIDC 1978; Stoker 1983; Pedersen et al. 1985; Stern 1985).

Annual catch estimates for the three years were:

Year	Harvest (lb)	Annual per capita catch (lb)
1973	21,000	105–131
1975	6,500	50
1985	12,700	58

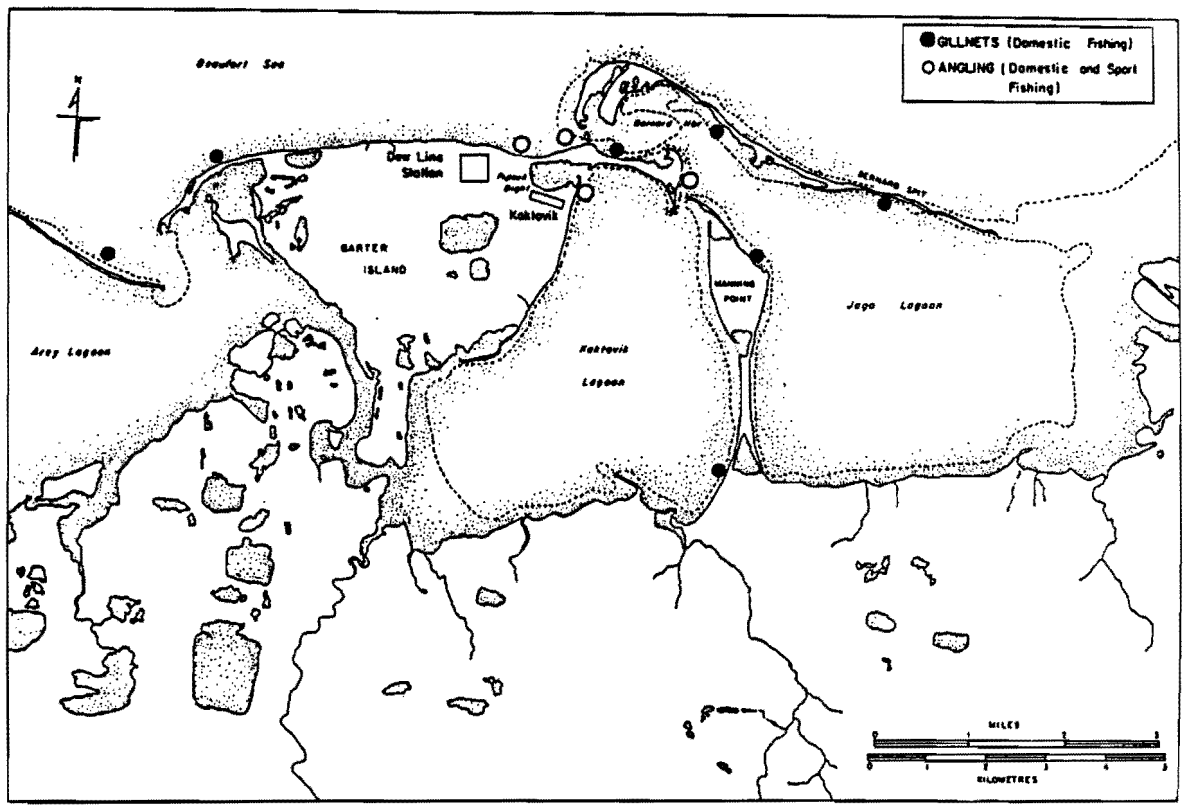

Figure 22. Kaktovik summer fishing sites in the vicinity of Barter Island, 1975. Source: Griffiths et al. (1977).

Patterson (1974) based his estimates on interviews with village representatives and estimated that the average catch during 1969–1973 was 15,000 pounds dressed weight or 21,000 pounds total weight (Table 4). This amounted to about 14 percent by weight of the total harvest of subsistence resources and an annual per capita catch of 131 pounds of fish. Stoker (1983) used Patterson's figures as the estimated annual harvest over the 20-year period 1962–1982, although he estimated that fish comprised about 22 percent of the total harvest of subsistence resources and that the annual per capita catch during this period was 105 pounds of fish.

Table 9. Kaktovik fishery, 1975 (source: Griffiths et al. 1977).

		Kaktovik fishery in 1975		
Location	Species	Estimate of 1975 catch	Average weight/fish (lb)	Estimate of total weight (lb)
Kaktovik	Arctic char	208	1.5	310
	Arctic cisco	1,722	1.3	2,240
	Arctic cod	1,250	0.07	90
Griffin Point	Arctic char and Arctic cisco	2,000	1.4	2,800
Hulahula	Arctic char	350	1.1	390
Lake Schrader	Lake trout	150	4.4	660
Totals		5,680		6,490

The 1975 harvest estimate was derived by Griffiths et al. (1977) from questionnaires and interviews with Kaktovik fishermen. Only three Kaktovik families responded to the questionnaires, but they represented approximately 40 percent of the village (population size of 130 in 1975) and 70 percent of the total fishing activity in 1975. The estimated total harvest that year was about 6,500 pounds, for an annual per capita catch of 50 pounds (Table 9).

Pedersen and Shishido (1988) based their estimate of the 1985–1986 fish harvest on interviews with 42 of the 54 households in Kaktovik. Although the data cover the period from July 1985 to June 1986, the data pertain mostly to 1985 because relatively little fishing occurred from January to June 1986 (Fig. 10). The 42 households reported catching 9,151 pounds of fish (Table 10). An expansion of these data to all 54 households in the village yields 11,700 pounds dressed weight or 12,700 pounds total weight. The annual per capita catch was thus about 58 pounds of fish in 1985.

Envirosphere (1986) also interviewed Kaktovik fishermen in 1985. Based on limited data, Envirosphere suggested that the summer harvest consisted of about 1,000–2,000 Arctic cisco and 2,000–4,000 Arctic char, which would equal 4,300–8,600 pounds of fish using the conversions listed in Table 10.

Table 10. Kaktovik fish harvest based on preliminary data from household surveys, July 1985–June 1986 (source: Pedersen 1987).

Fish	Estimated usable weight (lb)		Estimated total harvest		
	Sub-sample*	Total	No. fish caught†	Weight/ fish (lb)‡	Total weight (lb)
Arctic char	5,232	6,708	2,396	1.5	3,590
Arctic cisco	3,660	4,692	6,703	1.3	8,710
Grayling	167	214	238	1.2	290
Lake trout	92	118	30	4.4	130
Flounder	0.5	1	—	—	—
Totals	9,151	11,733	9,367		12,720

* Of the 54 households in the village, 42 (78%) were sampled.
† Derived from Pedersen's conversion factors.
‡ Derived from Kaktovik data (Griffiths et al. 1977) where possible; otherwise from Table 1.

DISCUSSION

Two points emerge from this review—fishing is an important component of the Inupiat subsistence economy, and the sizes of the harvests are not well documented. Although the Inupiat frequently participate in fishing activities (Kruse et al. 1981), fishing has received relatively little attention for two general reasons—it has less cultural significance than hunting (Wilimovsky 1956), and it is an activity that is not as easily quantified as are harvests of other major resources, particularly large mammals (caribou, bowhead whales).

There are several problems inherent in attempts to quantify fish harvests (AEIDC 1978; ADFG 1986):

1. Methodology. Estimates based on questionnaires or interviews with local residents are often not verifiable, and estimates based on on-site monitoring (usually in association with biological studies) may miss catches at remote fish camps or in seasons when biologists are not present.

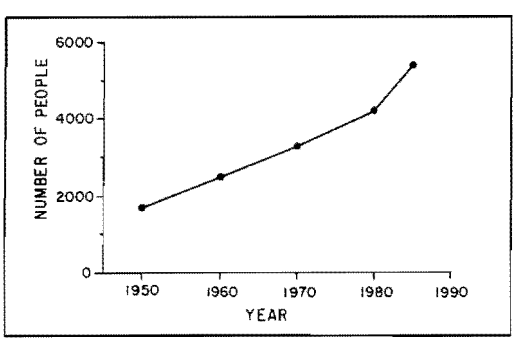

Figure 23. Number of North Slope residents (excluding oilfield workers in Prudhoe Bay and vicinity). Source: Kruse et al. (1981) and State of Alaska (Department of Community and Regional Affairs, FY 1986 Revenue Sharing Program).

Table 11. Estimated total harvest of fish at North Slope villages in 1985 (i.e., annual per capita catch × population size).

Village	Data year		1985 population estimate†	Estimated harvest in 1985 (lb)
	Year	Pcc (lb)*		
Barrow	1973	32	3,075	98,400
Wainwright	1973	9	507	4,600
Point Lay	1983	4	142	600
Atqasuk	1983	43	248	10,700
Nuiqsut	1985	241	332	80,000
Kaktovik	1986‡	58	220	12,700
Total weight (lb)			207,000	
Dressed weight (lb)§			165,000	

* Per capita catch (annual).
† Source: State of Alaska, Department of Community and Regional Affairs, FY 1986 Revenue Sharing Plan.
‡ Preliminary data from S. Pedersen (pers. comm.).
§ Charlie Brower (pers. comm.) notes that the whole fish (without gut) is often consumed. An average value of 80% usable weight is used here.

2. Annual variability. Harvests vary annually, reflecting changes in fish abundance or changes in fishing effort (e.g., some people may not fish every year if other sources of employment or other game species are available). Thus, a single year's estimate of the fish harvest may or may not reflect typical conditions.

3. Cultural considerations. Subsistence use of resources is a culturally significant activity the value of which is not measured by quantity alone.

Furthermore, changing patterns of resource use have been noted by some researchers. Nelson (1981), for example, comments about a resurgence in fishing activities at Wainwright. In addition, the steadily increasing population size in North Slope communities (Fig. 23) may also exert an increasing pressure on fish resources. Consequently, pre-1980 harvest levels probably do not reflect current conditions.

Despite these data limitations, it is apparent that fish are an important resource for the Inupiat communities. A rough estimate of the annual harvest (villages combined) is about 210,000 pounds of fish, or about 165,000 pounds dressed weight (Table 11). Although the total harvest of land and marine mammals is considerably larger than this, it is noteworthy that the utilizable weight of the fish harvest equals roughly 70 percent of the average harvest of bowhead whales at the same villages: 12 whales (the average number of whales landed each year; T. F. Albert, pers. comm.) × 19,580 pounds (the utilizable weight of each whale; Stoker 1983) = 234,960 pounds.

Given the continuing but underrated value of fish resources in modern Inupiat society, it is apparent that updated assessments of fish harvests are needed. For some

North Slope villages, the only available information about harvest quantities consists of one rough estimate made 15 years ago.

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Population Trends for the Arctic Cisco (*Coregonus autumnalis*) in the Colville River of Alaska as Reflected by the Commercial Fishery

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Abstract. The model developed for Colville River Arctic cisco was used to predict catches for 1982–1985. Results consistently overestimated actual catch-per-unit-effort but mimicked relative change in 3 out of the 4 years. New blind predictions were made that suggest an impending decline in the fisheries over the next 5 years followed by a period of marked increases. Independent information concerning year class strengths in recent years suggests that the model predictions may be reasonably correct.

If the model predictions are proven to be correct over the next 10 years, then the model's value is that, despite some obvious flaws, it will have illustrated that the information contained in historical fishery catch trends can be directly used for fishery management and impact assessment purposes. Marked changes in key parameter estimates may signal impacts from development or overharvest.

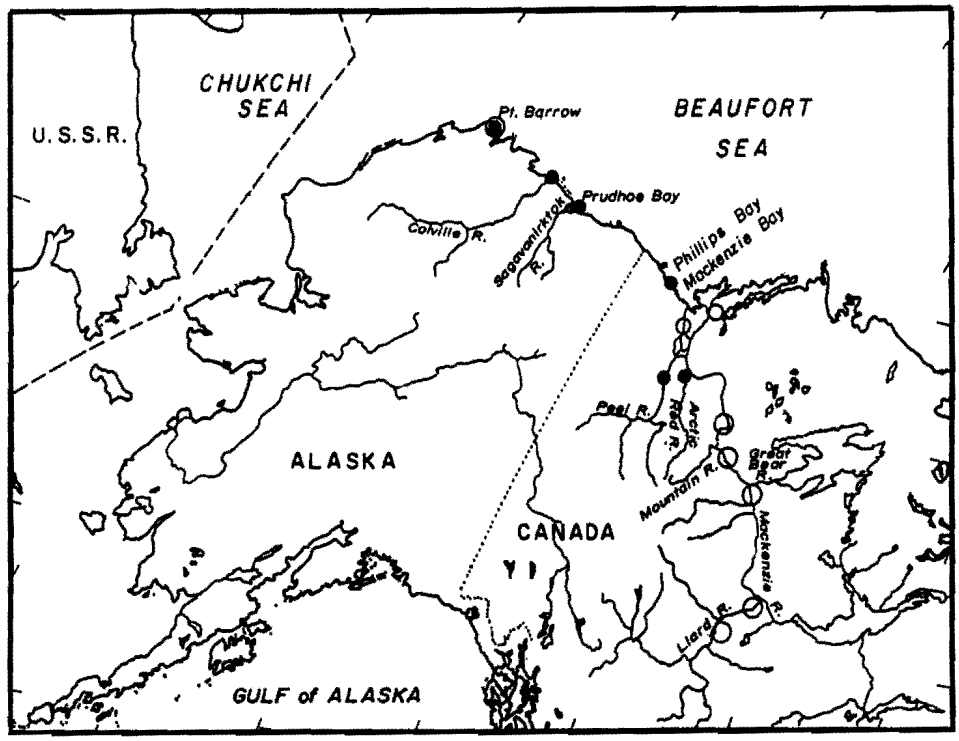
INTRODUCTION

The Arctic cisco, *Coregonus autumnalis,* supports commercial and subsistence fisheries in the central Alaskan Beaufort Sea, particularly in the Colville River delta during the fall season (Fig. 1A). The fish overwinter in the delta from fall to spring, then forage into food-rich coastal waters during the brief arctic summer. These foraging movements from the Colville River delta appear extensive, especially to the east. Arctic cisco from this delta are known to move eastward through the Simpson Lagoon system, into Prudhoe Bay, and then to and beyond the Sagavanirktok River delta, before returning to the Colville River delta towards the end of the summer. The extent of westward movements has not been well documented. By virtue of its size, the Colville River delta is the major overwintering site for arctic cisco in Arctic Alaska, although other river deltas (such as the Sagavanirktok River delta) have been documented to harbor smaller populations (Schmidt et al. 1989).

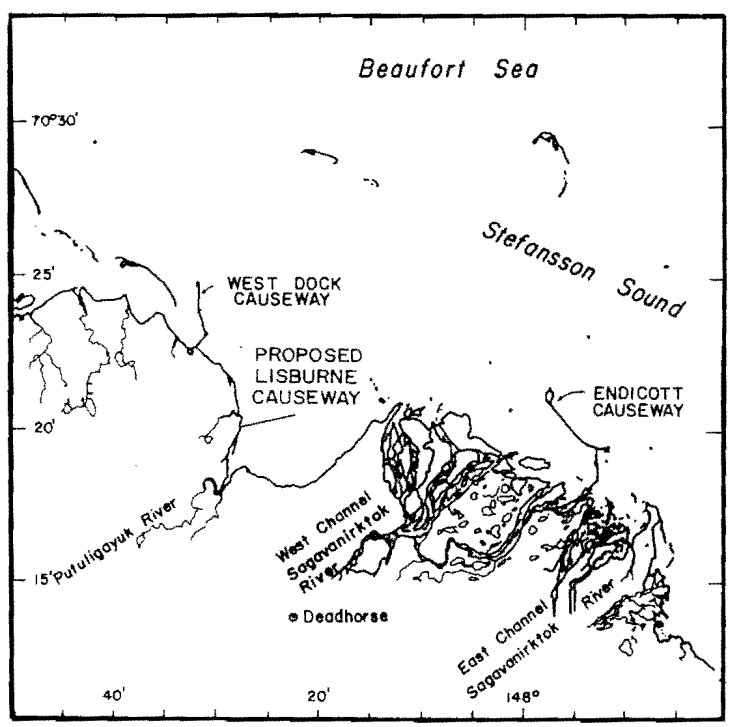
Given the commercial and subsistence importance of Arctic cisco, and the potential for hydrocarbon development to affect the fish, Gallaway et al. (1983) subjected this species to a population analysis. They used the Deriso (1980) model applied to catch-and-effort data from the Helmericks fishery. This one-family commercial fishery has operated in the Colville River delta of Alaska since 1967. The model yielded a sequence of catch-per-unit-effort (CPUE) values similar to the historical record, albeit with some exceptions (e.g., 1977). Two of the parameter estimates (an exceptionally low survival of catchable fish, and an exceptionally high level of fish invulnerable to the fishery) led to the hypothesis that the Alaskan population of Arctic cisco was an isolated portion of the stock (or stocks) associated with the Mackenzie River of Canada (Fig. 1A). The premise of the scenario was that some proportion of age-0 fish entering coastal waters from the Mackenzie River were transported by westward-flowing currents into Alaskan waters during late summer. Those that were able to locate suitable overwintering sites at river deltas would survive the first winter and then remain in association with that overwintering site until the onset of maturity (ages 7 and 8), when they would return to the Mackenzie River system to spawn.

This hypothesis provided a reasonable explanation for the apparently contradictory low survival and high invulnerability of catchable fish. It also explained other observed phenomena such as the age distribution of Arctic cisco in the Colville fisheries and the absence of any documented spawning by this species in Alaskan rivers (Gallaway et al. 1983). The evidence supporting this hypothesis has since been strengthened based upon results of genetic studies (Bickham et al. 1989), and documentation of the transport of age-0 fish from Canada to the Colville River (Moulton 1989).

Understanding of Arctic cisco biology has become a high priority given the importance of the species in northern Alaska and its potential for impact from causeway development in northern Alaska. Here, offshore hydrocarbon developments have used solid-fill causeways either as docks or to connect the mainland and offshore drilling and production islands. The existing causeways in this region are sited in the vicinity of Prudhoe Bay (West Dock) and the Sagavanirktok River delta (Endicott Causeway), both east of the Colville River (Fig. 1B). West Dock, constructed in 1975, was extended in 1976 and



A. Regional site map, note location of Prudhoe Bay relative to the Mackenzie and Colville River drainages.



B. Existing and proposed causeways in the Prudhoe Bay vicinity.

Figure 1. Regional site map (A) and detail map for the Prudhoe Bay region (B).

again in 1981 to a total length of about 4 km. The Endicott Causeway, constructed in 1984, also extends some 4 km seaward.

Concerns about the impacts of these causeways have been related to their potential to (1) block initial transport of age-0 fish, thereby preventing them from reaching the favorable overwintering sites (and the fisheries) in the Colville River delta; (2) prevent intermediate-aged fish

(ages 1–6) from the Colville River from foraging eastward beyond West Dock or those from the Sagavanirktok River delta to forage westward beyond Prudhoe Bay, thereby greatly reducing the extent of available feeding habitat; or (3) prevent the return migration to the Mackenzie River of mature fish from habitats west of the causeways. These structures, in addition to being potential barriers in themselves, alter circulation patterns and, in some instances, promote the intrusion of cold marine waters toward shore. Such changes have the potential to impose impassible barriers in an otherwise continuous, or nearly continuous, ribbon of habitat and reduce overall habitat quality.

Thus, by reducing habitat, causeways have the potential to affect population levels of Arctic cisco in Alaska, and perhaps even the source population in Canada. Evaluating the potential for these effects requires that the population ecology be well understood. The use of population dynamics models to predict natural fluctuations, and comparisons of model results with observed patterns, represents one approach toward this end.

The overall goal of this paper is to state an explicit hypothesis concerning how Arctic cisco populations are regulated, and, based upon this understanding, evaluate the potential threats from Alaskan fisheries and hydrocarbon developments. As with any scientific effort, the goal is not to prove the model, but rather to disprove it, if possible. The model is nothing more than a contextual framework enabling one to identify those areas that are critical to understand if a realistic assessment is to be reached, determine where we might be at present in that regard, and identify what more needs to be known. The assessment approach used herein differs from "gestalt" in really only one—but a major and an important way—the logic is made explicit and is testable.

The specific purposes of this paper are threefold. First, we test the model developed in 1983 by using it to make blind predictions of commercial fishery (Helmericks) CPUE for the subsequent period 1982–1985, and to compare these production estimates with the actual CPUE achieved by the fishery. Second, we evaluate the Gallaway et al. (1983) stock origin theory both in light of the model parameters and new information. Finally, we evaluate whether the existing fisheries and causeways have had observable effects on population levels of Arctic cisco.

In regard to the last objective, Gallaway et al. (1983) discussed the apparent effects of both the existing fishery and the West Dock causeway on the observed oscillations in estimated population levels of Arctic cisco, concluding that neither factor had been significant. In this paper, we evaluate these questions because (1) a new causeway has been constructed, and (2) there has been a major expansion in available fishery information for the region from the Sagavanirktok River delta to the Colville River delta. Critchlow (1983), Griffiths et al. (1983), Woodward-Clyde Consultants (1983), Biosonics, Inc. (1984), Moulton et al. (1985, 1986), George and Kovalsky (1986), George and Nageak (1986), and Cannon et al. (1987) have provided important new data for evaluating the effects of causeways and the fishery in the Colville River delta on Arctic cisco stocks.

MATERIALS AND METHODS

The Fishery

A detailed description of the Helmericks' commercial fishery in the Colville River delta is provided in Gallaway et al. (1983). Briefly, it is an under-ice gill net fishery using nets typically 2 × 50 m with either 7.6-cm (3-in) or 10.2-cm (4-in) stretched mesh. During the period 1967–1981, effort with the small mesh nets comprised over 98 percent of the total fishing time, while from 1982 to 1985 virtually 100 percent of the effort was with the small mesh nets. Historically, fish of age 5–8 have dominated the catch, and fish in spawning or spent condition have been rare.

Fishing begins in early October and ends in late November (Fig. 2). The nets are usually checked daily except Sundays, and detailed records are maintained.

Since 1981, the maximum number of nets fished per day has been 12. Prior to this, and excluding 1970 and 1979, about 20 or more nets were typically fished per day. The recent reduction in fishing effort is clearly shown along with corresponding catch levels in Figures 3A and B. During 1982 and 1983, fishing was restricted to the East Channel. In 1984, it was restricted to the Main Channel because of unfavorable ice conditions in the East Channel. In 1985, total effort was split between the two channels, with 192 of 363 total net days expended in the Main Channel.

The Model

This paper applies the Deriso model as parameterized in Gallaway et al. (1983) using catch-per-effort data from Helmericks' commercial fishery to estimate catches for 1982–1985. The model, simply stated, says that a given year's biomass will be the survivors of the previous year's stock, corrected for weight growth, plus new recruits. When numbers instead of biomass are modeled, the model is expressed:

$$C_{t+1} = \ell(1 - qE_t + m)C_t - \ell^2 m(1 - qE_{t-1})C_{t-1} + q(1 - m)R[(1 - qE_{t-1-k})C_{t+1-k/q}],$$

where the variables are:

C_t = CPUE during year t,
E_t = effort during year t, and
$R(.)$ = recruitment function with $R(s) = se^{\alpha - \beta s}$ (Ricker curve),

and the parameters are:

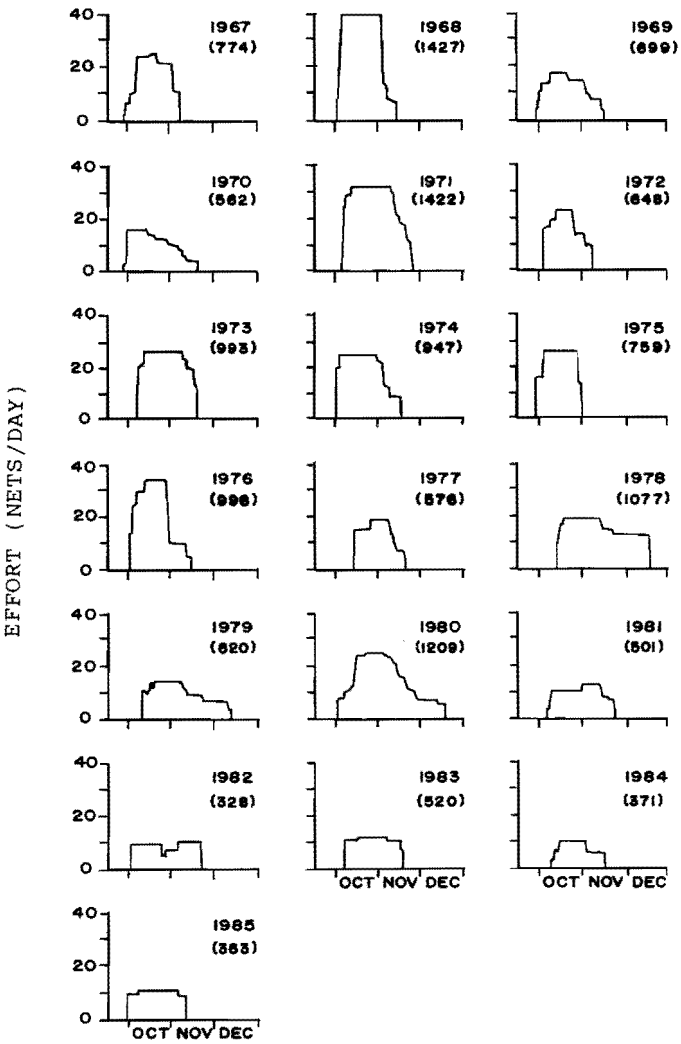


Figure 2. Patterns of daily commercial fishing effort for the Helmericks' commercial fishery, 1967–1985. Data for 1967–1985 from Gallaway et al. (1983). Number in parentheses represents total net-days.

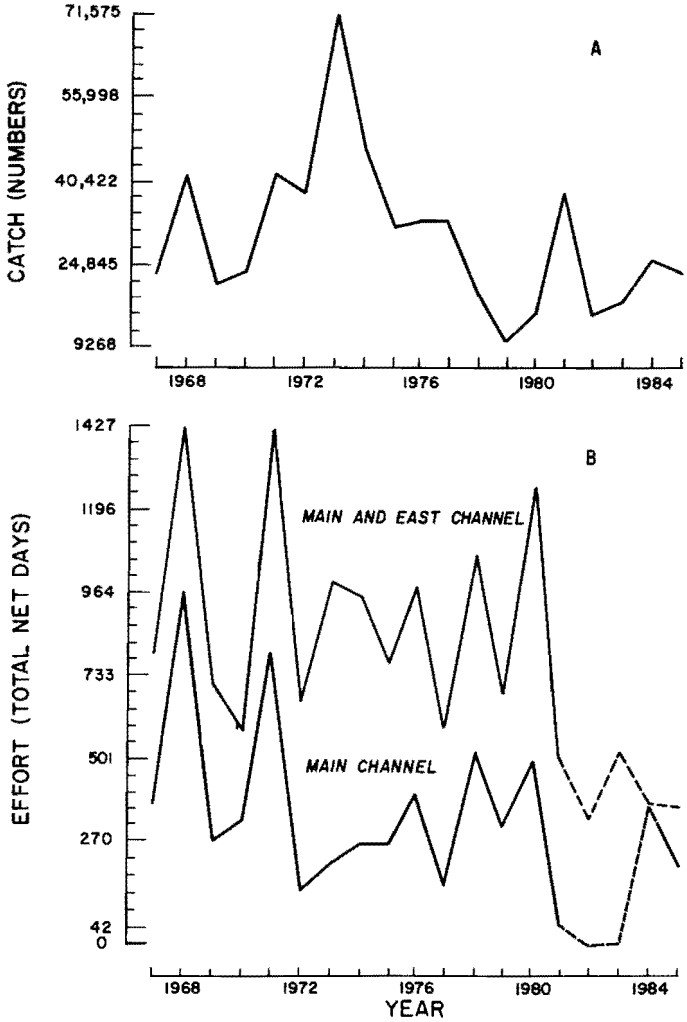


Figure 3. Patterns of annual catch (A) and fishing effort (B) for the Helmericks' commercial fishery, 1967–1985.

ℓ = annual natural survival,
q = catchability coefficient,
α, β = Ricker recruitment parameters,
$1 - m$ = fraction of recruits vulnerable to fishery (allows for incomplete recruitment), and
k = lag time between birth and recruitment (k + 1 = age at recruitment).

The survival term (ℓ) relates only to the catchable population; the early life history (noncatchable fish) is summarized in the model by the stock–recruit relationship in conjunction with k, lag time between birth and entry into the fishery.

Standard errors for the parameters were not calculated in either the original paper or this one. The only available method for doing so is a linearization about the solution values, which results in underestimates of either standard errors, or the correlation between parameters, or both (especially for small sample sizes). Therefore, the variance–covariance values that would lead to model acceptance or rejection would be based more on statistical approximation than on true model performance. The best method for model evaluation was believed to be blind prediction and the biological reasonableness of parameter estimates.

Before proceeding, one needs to consider the sensitivity and role that each parameter plays in the Deriso equation. The parameters can be conveniently classed according to their major effect upon the model as either scaling or dynamic parameters. The scaling parameters consist of q, ℓ, and β. The catchability coefficient (q), which relates CPUE to population level, has the major effect of moving the entire time trend of CPUE either up or down on the y-axis. Statistically, q is very well determined within the context of the available data, and comparisons of the model estimates of "q" with independent studies can be made easily. Interpretation, however, is difficult since gear selectivity and small differences in gear effectiveness can

produce very large shifts in the computed value of q from study to study. Survival (ℓ), which strongly controls the trend of CPUE over time, requires a long time series to estimate accurately but should be directly comparable to estimates obtained using other approaches. The Ricker recruitment parameter controls the magnitude of recruitment to the catchable population. Unfortunately, studies that address recruitment are rare, and independent comparison of parameters will seldom occur.

The dynamic parameters consist of k, α, and m, which control the oscillatory behavior of the model. The overall behavior is most sensitive to the recruitment lag (k). Fortunately, the value of k can easily be confirmed with data on age of fish. The remaining two parameters (m, the fraction of recruits invulnerable to fishing, and α, which controls the shape of the Ricker recruitment curve) are the best indicators of biological reasonableness, once k has been verified. Agreement of either parameter with independent studies should be viewed as biologically significant.

Gallaway et al. (1983) parameterized the Deriso model using the time series of catch data from Helmericks' commercial fishery taken from 1967 to 1981. Quasi-linearization and nonlinear Newton's methods were used to estimate the parameters (Deriso 1980; Walters 1981) such that the predicted sequence of CPUE values agreed best with the observed sequence. Because the model is recursive, these parameters can now be used to project future levels of CPUE, either "blind" or by using either known (or estimated) effort or catch to drive the model.

We elected to make the projections of 1982–1985 CPUE blindly, i.e., without benefit of the known level of effort or the actual catch values for the 1982–1985 period of record. Instead of using fishing effort as a driving variable for projecting CPUE, we substituted the quantity qE_t with c_t/qC_t, where c_t is the catch and C_t the predicted CPUE from previous recursions. Similarly, all occurrences of actual CPUE were replaced with predicted CPUE. The projections of CPUE required only the single input of the previous year's catch since, conceptually, last year's catch is subtracted from the standing stock before a prediction is calculated. Because the model is recursive, previous discrepancies between model and actual CPUE will again surface in the predictions.

RESULTS AND DISCUSSION

The Fishery

Catches of Arctic cisco have varied over the years. With the exception of the 1969 and 1981 peaks, catches of Arctic cisco since 1977 have been low compared with catches taken during the period 1967–1971 (Fig. 3A). Catch declined markedly in 1982 from the previous 1981 high, then increased in 1983 and 1984 (Fig. 3A). Catch in 1985 was slightly lower than in 1984.

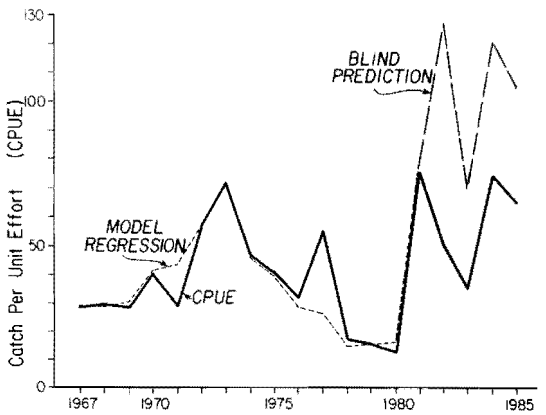


Figure 4. Population trends of Arctic cisco (*Coregonus autumnalis*) based on CPUE (1967–1985), model regression (1967–1981), and blind prediction (1980–1985).

CPUE values for Arctic cisco (Fig. 4) do not reflect a sustained period of low population levels, as might be inferred from the catch data above (Fig. 3A). CPUE increased from 1967 to a record high in 1973. Following 1973, there was a precipitous and steady decline through 1980, except for a pronounced peak in 1977. CPUE values for 3 of the 5 years since 1980 have exceeded all but one (1973) of the historical highs. CPUE for the other two years have been in the midrange of historical values (Fig. 4). The overall reduction in Helmericks' catch in recent years thus appears more related to decreases in fishing effort than to population declines.

Model Results

Simulations

Comparisons of blind predictions with actual CPUE for 1982–1985 fail to invalidate the model. The blind predictions consistently overestimate actual CPUE, but mimic relative change in CPUE in 3 out of the 4 years (Fig. 4 and Table 1). Overall the model fit was impressive (Kendall's Tau = 0.9, $P < 0.001$) but, alternatively, any function with five parameters can exhibit remarkable flexibility. Although three out of four successful blind predictions is not statistically significant ($P < 0.31$, binomial sign test), the year "missed" with regard to predicting the CPUE was 1982 (model CPUE greater than actual CPUE), which was a predictable error given the model's 5-year periodicity and the previous discrepancy between model and actual CPUE that occurred in 1977.

Given the uncertain outcome of the blind predictions with regard to invalidating the previous model, we elected to update the parameter estimates by including the 1982–1985 catch and effort data and make new blind predictions for the future catches. The results were somewhat surprising (Fig. 5 and Table 1). Although the new parameters produce results that are better scaled and where actual and modeled CPUE levels once more generally

Table 1. Parameter values.

Parameter	Previous estimates* (Fig. 4)	All data, no CPUE adjustment (Figs. 5, 7)	All data, adjusted CPUE for 1977 and 1982 (Figs. 6, 7)
k (recruitment lag)	5	5	5
ℓ (survival)	0.37	0.19	0.23
$q \times 10^{-4}$ (catchability coefficient)	3.3	3.8	4.0
α (recruitment parameter)	4.8	4.0	4.5
$\beta \times 10^{-5}$ (recruitment parameter)	5.5	4.3	5.6
m (recruits invulnerable)	0.64	0.63	0.67

* Gallaway et al. 1983.

agree, the dynamics of annual catch patterns are more poorly represented in this regression than in the original model. In this new model version, CPUE for 1978, 1980, 1981, 1982, and 1984 (in addition to those of 1971 and 1977 in the original version) appear different from actual CPUE. Both regressions require k values of 5 and produce similar estimates of the invulnerable fraction of the stock (0.64 versus 0.63; Table 1). Agreement between modeled and real CPUE values was achieved by decreasing the survival rate and increasing the catchability coefficient. That these scaling factors require modification is not surprising, because they typically require a long history of time series data to estimate accurately. Initially, the data record extended over only 15 years; now it extends over 19 years. The assumed lag of 5 years to recruitment allows only 14 points (versus 10 points originally) to fit five parameters.

As noted above, oscillatory behavior of the model is influenced by the α parameter of the stock–recruitment relationship. The model appears extremely sensitive to reduction in the strong density dependence relationship as evidenced by the decreased ability of the total regression (Fig. 5) to capture the fluctuations of observed CPUE

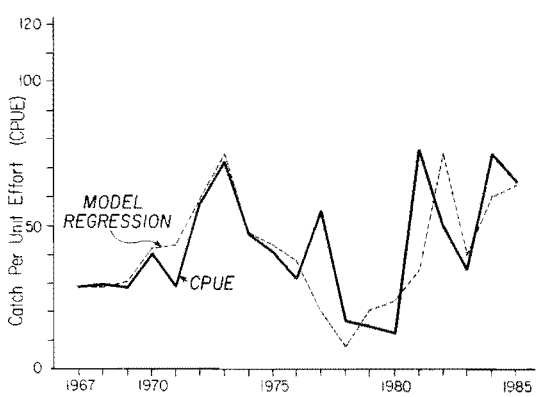


Figure 5. Model regression based on all CPUE data (1967–1985).

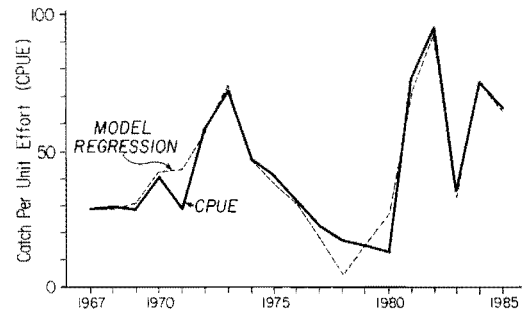


Figure 6. Model regression based on altered CPUE data (1977 and 1982 changed to 22.0 and 95.0, respectively).

patterns as compared to the original model regression (Figs. 4 and 5).

Review of the model results versus actual CPUE data suggests that the catch data that seem to invalidate both the old and new regressions were collected in 1977 (high actual versus low model CPUE) and in 1982, 5 years later (low actual and high model CPUE). The high actual 1977 CPUE value had not been captured in our original model, nor was it suggested from independent population estimates conducted over the period 1976–1981 (see Fig. 6; Gallaway et al. 1983). With a 5-year lag, this previous discrepancy would be expected to surface again in 1982. Therefore, we assumed that CPUE values for some years might not be representative of the abundance of catchable fish in the delta. As a test of this idea, we assigned "representative" values of CPUE for 1977 and 1982, and regressed the model on the resulting database (Fig. 6 and Table 1). An impressive fit was achieved when the actual CPUE data for the two anomalous years were adjusted, confirming that data for these 2 years are the principal source of the problem, assuming possible model validity.

The models based upon the regression containing actual CPUE data (1967–1985) (Fig. 5) and the CPUE data adjusted for years 1977 and 1982 (Fig. 6) were used to make blind predictions of future stock levels (Fig. 7). The projections suggest that CPUE in the Colville Delta fishery will decline markedly in either 1986 or 1987 and

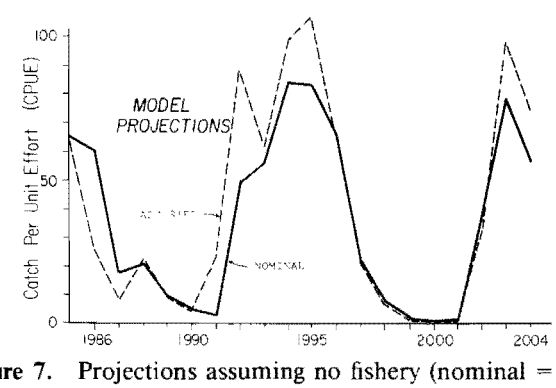


Figure 7. Projections assuming no fishery (nominal = based on regression with all CPUE data, adjusted = based on regression with 1977 and 1982 data years ignored).

remain relatively depressed through 1990 or 1991 (Fig. 7). Thereafter, CPUE should increase and remain high until about 1996, after which another period of low CPUE will continue through 2000. Had the model run in 1985 not predicted the marked declines observed in 1986 and 1987, we would have questioned its validity.

The model predictions through 1990 can be evaluated to some degree at present. The most recent high catches are due in large part to a strong 1979 year class, as documented by a number of authors (e.g., Griffiths and Gallaway 1982; Critchlow 1983; Moulton et al. 1985). In the intervening years, recruitment of young Arctic cisco into central Alaska was apparently low until the summer of 1985. In 1985 and 1986, transport of age-0 Arctic cisco into central Alaska was high as will be discussed below. The combination of this independent information suggests the model projections for the 1986–1990 period may be reasonably correct. However, CPUE in 1986 was high, and included many fish considered small for their age (L. L. Moulton, pers. comm.). Researchers monitoring the fishery there do note that a further decline appears probable for 1988.

Biological Evaluation of Model Parameters

Another way to evaluate a model in which a set of parameters is estimated from a series of catch data is to compare the model parameter estimates to estimates obtained from independent data by conventional methods. The model may provide a "nice" fit but if the parameters providing the fit are outside the bounds of biological reasonableness, the model is obviously invalidated.

The model is exceedingly sensitive to changes in "k", the lag from birth to recruitment. Only $k = 5$ will "work," suggesting that fish should enter the fishery at age 5. We are aware of age composition data from the Helmericks fishery from two sources, Craig and Haldorson (1981), covering 1976–1978, and Moulton et al. (1986), covering 1984 and 1985. Age-6 Arctic cisco dominated the catches in 1976, 1978, and 1985, but age-5 fish dominated in 1977 and 1984. Age-5 fish likely also dominated the 1979 catches, based on a fish modal length of 280 mm (see Table 26 in Craig and Haldorson [1981] for length–age relationships). Thus, actual age of recruitment of Arctic cisco into the Colville fishery is age 5. The independently estimated model parameter $k = 5$ is therefore reasonable.

Much of the model's oscillatory behavior is controlled by the stock–recruit parameter α, which at 4.0–4.8 suggests a strong density-dependent relationship, yielding a very peaked recruitment curve. Such a curve suggests that at high stock levels there is a "scramble" for some limiting requisite (e.g., food or oxygen) with few or none of the progeny getting enough to complete development (Ricker 1975). At low stock levels, reproduction rate may be reduced or there may not be enough progeny for many to escape predation or other causes of mortality. If the dynamics are being controlled in this manner, one must assume that transport conditions are rather consistent from year to year since all the estimates are based upon Alaskan fishery data only. The recruitment curve indicated by the model may be correct, and the lack of fit during some years might be attributable to random variation in generally consistent transport conditions.

Gallaway et al. (1983) suggested that a similar pattern could result from the conceptual model of Arctic cisco life history the authors proposed, in which the oscillatory behavior might be simply a function of favorable transport conditions. Conditions for westward transport were highly favorable in 1985, for example. Ice conditions that year were unusual in the Mackenzie Delta area (D. Fissell, Arctic Sciences Limited, British Columbia, Canada, pers. comm.). Ice was present all along the Tuktoyaktuk Peninsula but open water was present to the west in conjunction with strong easterly winds throughout the summer. For the first time, a group of age-0 Arctic cisco was tracked from the Yukon Coast (W. Bond, Freshwater Fisheries Institute, Winnipeg, Canada, pers. comm.) to Barter Island and through the Prudhoe Bay vicinity (Cannon et al. 1987) and, ultimately, to the Colville River (Fawcett et al. 1986). Furthermore, catch rates for this size group in central Alaska were the highest recorded in any of the recent studies, with over 5,000 fish recorded in a single daily fyke-net catch (Cannon et al. 1987). Fawcett et al. (1986) reported that the calculated rate of movement of this size group of young Arctic cisco corresponded to the theoretical estimates of passive drift proposed in the stock origin theory (Gallaway et al. 1983). Variability in transport conditions as an alternative to a density-dependent stock–recruit relationship for explaining Alaskan fluctuations in Arctic cisco populations remains attractive. Preliminary analyses correlating catch with percentage of time summer winds at Barter were from the east 5 years prior to the year of catch are also suggestive of a strong relationship, especially when ice distributional patterns are considered.

Acceptance of transport conditions as being the primary factor controlling the abundance of Arctic cisco populations in Alaska implies that the fluctuations in population levels of this species in Alaska are random in nature and density independent. While the fluctuations may be density independent, they do not appear random. An alternative density-independent hypothesis following Shumilov (1971) is outlined below. This hypothesis incorporates some features that would suggest that the variation in abundance levels of Arctic cisco in Alaska is not purely random.

Shumilov (1971) and other Russian colleagues have provided a rather convincing argument that the apparent density-dependent stock recruit relationship that they observed for a North Baikalian population of Arctic cisco (see Fig. 2 in Shumilov 1971) was actually attributable

to spawning-stream water level, or discharge factors, having a 5-year cyclicity. They believe that the discharge patterns vary in conjunction with solar activity cycles. Shumilov (1971) proposes that high water levels in fall and winter serve to (1) enable the spawning fish to reach higher quality spawning grounds, and (2) reduce the egg mortality arising from the effects of bottom ice and freezing, respectively. Low water levels in spring were believed to promote larval survival. Under high-water conditions, Shumilov (1971) believed that large numbers of larvae were carried away from the river bed into lakes and flooded areas of the floodplain where they remained for a long time and were more intensively cropped by predators. The combination of river levels during the spawning period and the downstream migration of larvae was deduced to predetermine the strength of the year classes ultimately entering the fishery. The periodicity of solar activity affecting hydrological cycles resulted in Arctic cisco catches fluctuating on a 5-year cycle.

The CPUE patterns in the Helmericks fishery do not reflect a 5-year cycle in abundance patterns (Figs. 4–7). While the observation of strong year classes in 1979 and 1985 with weak year classes in the intervening years does lend some support to the hypothesis of a cyclic abundance, the interval is 6 not 5 years.

Whatever the reason, the historical catch data (1967–1985) exhibit a predictable cycle. The cycle is well described by a density-dependent stock–recruitment curve, but it could also be attributable to density-independent phenomena having a regular cycle, at least to date. In either case, variation in conditions favoring westward transport may obscure the cycle; that is, during some years characterized by strong year classes few may be transported into Alaska and vice versa.

The model parameter "m" (proportion of recruits not vulnerable to the fishery) was high, ranging from 63 to 68 percent, suggesting that the overall mean proportion of the Mackenzie River production of Arctic cisco annually transported from Canada to Alaska falls between 32 and 37 percent, a rather narrow range.

Fissel and Birch (1984) estimated that proportions of total river discharge through the main Mackenzie River delta distributaries were 38 percent into western Mackenzie Bay, 28 percent into eastern Mackenzie Bay, and 34 percent into Kugmallit Bay. In Mackenzie Bay, there is known to be a persistent divergence in flow, with one of the currents flowing northwest from the west side of the bay toward Herschel Island (Herlinveaux and de Lange Boom 1975; MacNeill and Garrett 1975; ESL 1979). Thus, although the flow of the Mackenzie River water during the open-water season is generally northeasterly (see ESL 1979; Fissel and Birch 1984), there is a consistent current to transport to the west young Arctic cisco discharged into western Mackenzie Bay. Assuming that young fish are transported in direct proportion to flow, about 38 percent of the total might be transported toward Alaska. Significant variation in transport capability might occur only when the proportion of easterly winds substantially deviates from the long-term mean.

The model estimates of q, the catchability coefficient, ranged from 0.0003 to 0.0004. Calculations of "q" based upon mark–recapture data (Moulton et al. 1986) suggest that during 1984 and 1985, catchability was 0.000075 and 0.000056, respectively. These are an order of magnitude lower than the model estimates. However, the mark–recapture estimates are based upon recaptures in the fall fishery of fish marked and released the preceding summer in the Prudhoe Bay region. While the release sample is corrected for gear-selectivity differences between the fishery (gill nets) and the summer marking effort (fyke nets), no adjustment has been made for fish marked in the Prudhoe Bay area that do not return to the Colville River delta. Such fish would include a small number that overwinter in the Sagavanirktok River delta (approximately 3,000) and other rivers, as well as those fish that pass through the area in the return migration from the Colville to the Mackenzie River for spawning. If one assumes the model estimates of q are correct, then the percentage of Arctic cisco that are tagged in the Prudhoe Bay region but are unavailable for recapture in the Colville River delta that fall must be high, on the order of 80 to 85 percent. Intuitively, 80 to 85 percent seems high, but this will be addressed further below.

In 1985, an extensive tagging program was conducted in the Prudhoe Bay region, including the tagging and release of over 11,600 Arctic cisco (Cannon et al. 1987). Importantly, remote recapture stations were operated during summer to the east (Kaktovik) and west (Oliktok Point). Further, other summer fish sampling programs were conducted in 1985 including one in the vicinity of the Colville River (Fawcett et al. 1986) and one in the eastern Alaskan Beaufort Sea by the US Fish and Wildlife Service (see Cannon et al. 1987). During summer 1985, only 129 Arctic cisco (1% of the release sample) were recaptured in the Prudhoe Bay region where they had been marked. A total of 10 Arctic cisco were recaptured at remote locations to the east and west of the region—four at Oliktok Point near the Colville River to the west and six to the east in the Kaktovik/Griffin Point area. Assuming that these returns of large Arctic cisco in remote areas east and west of Prudhoe Bay during summer might be representative of the proportions of the population returning to the Colville River delta versus the Mackenzie River yields an estimated 60 percent of the fish marked in summer in the Prudhoe Bay region that may have been travelling through the area in a return migration to the Mackenzie River. Further, five fish tagged in summer 1985 were collected in Canadian waters during summer 1986. If these fish migrated in 1985, then escapement would have been 73 percent. If these estimates are correct, the mark–recapture estimates of q (and exploitation rates) for the Colville River may be considerably underesti-

mated since the population level would have been greatly overestimated.

Given q, fishing mortality (F) can be derived simply based upon the effort data (E) using $F = qE$. Mean fishing mortality ($F = qE$) for the period 1982–1985 based upon $q = 0.0004$ and a mean effort of 394 net-days was 0.158. For 1985, F was 0.145. Rate of exploitation ($u = 1 - e^{-F}$; Ricker 1975) of Arctic cisco by the Helmericks fishery in 1985 was thus 13.5 percent, as compared to 14.6 percent for the 1982–1985 period.

Mean fishing effort in the Helmericks fishery during 1967–1985 was 778 net-days per season. Assuming $q = 0.0004$, mean fishing mortality was 0.31, which equates to an overall exploitation rate of about 26 percent. As noted above, there has been a decrease in exploitation rates in recent years to about half the former levels, at least for the Helmericks fishery.

Based upon the model, the historical exploitation rate of Arctic cisco by the Helmericks fishery has averaged about 26 percent, but in recent years the model estimates this fishery exploits only about 13.5 to 15 percent of the population. In 1985, Moulton et al. (1986) found that the Helmericks fishery accounted for 34 percent of the total catch of Arctic cisco in the delta. Based upon the model estimate of exploitation by the Helmericks fishery, total exploitation rate in 1985 by all the fisheries would have been on the order of 40 percent of the population.

Using population estimates based upon results of mark–recapture studies in 1985 in conjunction with actual harvest rates, Moulton et al. (1986) suggested total exploitation was only 6 percent. Historically, Craig and Haldorson (1981), also based upon mark–recapture analyses and harvest, estimated the Helmericks fishery to exploit on average about 9 percent of the population with the range being between 4 and 18 percent. In light of these, the model estimates seem high. However, the tag loss factor described above suggests that exploitation rates derived from mark–recapture studies may be underestimated due to inflated population estimates. To resolve this issue would require that a within-season mark–recapture study be conducted during the fishing season.

The model estimates for annual natural survival (ℓ) are low, but existing data suggest them to be realistic. Assuming $\ell = 0.23$ (model estimates range from 0.19 to 0.37; Table 1) and $u = 0.26$, total annual mortality (or rate of disappearance) is estimated at 0.83 ($A' = 0.26 + 0.77 - (0.26 \times 0.77)$; Ricker 1975). What if the exploitation rate is not 0.26, but rather either 0.40 or only 0.05? Given the former (0.40), total annual mortality is 0.86, and with the latter (0.05), total annual mortality is 0.78. Thus, it seems readily apparent that fishery exploitation rates from as low as 5 to as high as 40 percent of the harvestable pool have little impact on the overall annual rate of disappearance. Viewed in another way, escapement is high (on the order of 80%). Any one of the estimates (0.78–0.86) reasonably corresponds to the mean estimate of 0.80 deduced by Moulton et al. (1986) based upon mark–recapture studies in the Colville Delta.

Based upon $A' = 0.83$, the instantaneous rate of disappearance or total losses (Z') is estimated at 1.77[$Z' = -\log_e(1 - 0.83)$]. Given $F = 0.31$, then $M = 1.46$. If $A = 0.78$, then Z' is 1.51. Given $F = 0.04$ (778 net-days $\times$ 0.000056), M would be 1.47. Thus, while the annual loss rate of Arctic cisco from the Colville Delta appears to be high, losses to the Alaskan fisheries account for only a small proportion (3–18%) of the total loss. An explanation for the high loss rate is that, once the fish reach ages 7 or 8, they return to the Mackenzie River to spawn, as described in the next section.

Support for the hypothesis that maturing Arctic cisco leave the system comes from two sources—the earlier (Gallaway et al. 1983) and continued (Cannon et al. 1987) recapture of Arctic cisco tagged in the Prudhoe Bay area being taken in the eastern Beaufort, suggesting eastward movement, and from genetic analyses comparing allele frequency patterns for Arctic cisco from the Colville River delta fishery to fish spawning rivers in the Mackenzie drainage (Bickham et al. 1989). Allele frequency patterns for Arctic cisco from Mackenzie spawning rivers in the Mackenzie River basin were in Hardy-Weinberg equilibrium (i.e., distinct stocks), whereas those for Colville River fish were not, indicating mixed stocks there. If the Colville River population represented a separate spawning group, then Hardy-Weinberg equilibrium would have been expected. Lastly, there is no new direct evidence suggesting any appreciable level of spawning by Arctic cisco in Alaska.

Of the five model parameters, recruitment lag (k) and survival (ℓ) appear well supported by independent data. The parameters q (catchability coefficient) and m (recruits invulnerable) appear to be within reasonable bounds, although q appears high, and there are no real data for evaluating m. The recruitment parameters are within reasonable bounds, but environmental factors at the time of spawning and larval transport appear to determine year class strength of this species in Russian studies, and the same could be true for populations in western North America. The favorability of conditions for westward transport of age-0 fish is undoubtedly an important factor accounting for fluctuations in abundance in Alaska and may obscure regularly occurring cycles. The model would likely be substantially improved by incorporating functional larval survival and regional transport submodels instead of trying to summarize the early life history using a simple stock–recruitment relationship.

Evaluation of the Stock Origin Theory

The Gallaway et al. (1983) stock origin theory proposes that Arctic cisco spawning is restricted to rivers within the Mackenzie River drainage, with cisco migrating to Alaskan waters as follows. Age-0 cisco emerge and are

carried down the Mackenzie in the spring. Some enter the coastal zone, though large numbers have also been found in delta lakes (Taylor et al. 1982). Once in the coastal zone, these fish, too small to be strong swimmers, are presumed to be distributed eastward and westward along the coast by the prevailing currents. An unknown proportion of these fish is carried westward, ultimately colonizing Alaskan river deltas in late summer and fall where they overwinter in brackish areas (5 ppt and higher). There is some evidence that, once established in a delta, the fish reenter the delta each fall to overwinter (Moulton et al. 1986). Each subsequent summer, the fish disperse from this delta into coastal waters for feeding. But at the onset of maturity, they are believed to return to the Mackenzie River system for spawning.

By virtue of its large size, the Colville River delta would be expected to be the most suitable Alaskan habitat for overwintering anadromous cisco. Other deltas are smaller and contain limited areas of the deep channels necessary for fish to survive the winter.

Results of recent studies lend support to the stock origin theory proposed for Arctic cisco. In 1985, young Arctic cisco were documented to move westward as a sequential wave of abundance across the North Slope from the Yukon Coast to the Colville River as previously described. Therefore, the concept that some (or all) of the Arctic cisco in Alaska originate in Canada remains the best explanation of their distribution in north Alaska. Although it is still limited, tag return information documents the return of adult fish to Canada.

Earlier, we estimated what proportion of the Canadian Arctic cisco production might be from fish utilizing Alaskan habitats; rationale developed from model parameters and flow patterns led to an estimate of some 30 to 40 percent. Results of preliminary genetic work (Bickham et al. 1989) may provide the means to test the hypothesis without having to conduct an expensive field program covering several to many years. At present, fish from different spawning sites in the Mackenzie River system can be differentiated from one another, but the resolution of the data is not adequate to assign a given fish from a mixed collection in coastal waters to one of the identified stocks. Further, it is unlikely that all the stocks in the river system have been identified. Eventually, obtaining the required resolution to identify origin of the fish appears to be possible given continued genetic studies. With this resolution, one would be able to determine not only the proportional size of each stock but also how fish from each stock are distributed across the North Slope.

Impact Assessment Considerations

Virtually all of the studies conducted on arctic anadromous fish in Alaska over the last decade have been funded to support impact assessments, beginning with the offshore oil and gas lease sales and, in more recent years, for specific developments. This modeling study and its predecessor (Gallaway et al. 1983) have focused on the population dynamics of Arctic cisco using a recently published model (Deriso 1980). The model was not developed for impact assessments, but rather as a procedure for estimating the key parameters that control population success. Once these parameters are identified, it is a logical extension to examine them in terms of their implications to impact assessments—assuming the model provides credible outputs.

The most compelling feature about the model at present is that the parameter estimates are within the bounds of reason, and independent field observations provide a strong case that the model predictions of an imminent decline in the fishery—with the depressed catches lasting several years, after which there will be several consecutive years of high catches—may be expected. Based upon fykenet catches, very weak recruitment of young Arctic cisco into central Alaska was indicated for most of the years 1981–1984 (1983 was a possible exception), and very strong year classes have been observed for both 1985 and 1986. Assuming that these fish constitute the same fish that will ultimately be harvested by the fishery suggests the model has some credibility.

The model, as parameterized, suggests that the Beaufort Sea stock of Arctic cisco is predominantly controlled by a strongly density-dependent stock–recruitment relationship and that a large fraction of the stock is invulnerable to the fishery. The latter seems highly plausible since the main fishery for Arctic cisco occurs in central Alaska and is far removed from the Mackenzie River source area where the species is not highly esteemed or sought after by any major fishery. The proportion of the stock remaining in that area apparently is not subject to any heavy fishing mortality. A key question is what proportion does remain near the source river? The model's estimates of the invulnerable fraction range from 0.63 to 0.67, implying that 33–37 percent of the recruited stock may be vulnerable. Presumably the Colville River stock represents the vulnerable fraction.

It appears clear that the eventual recruits to the fishery are transported into Alaskan waters as late young-of-the-year, where they grow and mature for some 5 years before entering the fishery. They are then subject to the fishery for only 2 years, generally disappearing at about age 7. The good correlation between fishery catches and wind conditions in the eastern Beaufort Sea 5 years earlier (Fechhelm and Fissel 1988) supports the contention that Alaskan stock sizes may be mainly dependent upon transport conditions. If that is the main controlling factor, then variation in transport conditions for the period of record has mimicked the stock level pattern that would result from a density-dependent stock–recruitment relationship as suggested by the model. If this scenario is true, the model could be "right," but for the wrong reason.

If Arctic cisco populations are controlled by a strong

density-dependent recruitment curve, the potential for causeway and fishery effects would be (1) mainly restricted to periods when the stock was low, and (2) a function of the size of the fraction of the stock that is transported to Alaska. If the overall fraction is low, the potential for overall population impact would be negligible. However, we have estimated that the fraction might be, on average, on the order of 30–40 percent. If this fraction is correct, population-level effects could occur, especially during low stock levels.

With the above in mind, we now turn our attention to the impact assessment implications, assuming model validity. The first interpretation is that the high rate (0.80) of annual "mortality" suggests that mature or maturing fish are successfully leaving the system. The model estimate of total annual mortality (actually believed mainly to represent escapement) has been confirmed by independent mark–recapture estimates. Tag recapture information has shown that fish from the Colville River/Prudhoe Bay region are being taken in Canadian waters despite limited sampling effort. This, in conjunction with results of movement studies around causeways in the Prudhoe Bay region, suggests that return migrations are not being appreciably affected by the causeways in the Prudhoe Bay region. If return migrations do become affected, there should be a marked shift towards older-age fish in the age structure of Arctic cisco taken by the Colville fishery.

If the presumption of a high rate of escapement is correct, fishing mortality appears inconsequential. Varying fishery exploitation rates between 5 and 40 percent caused the overall total annual mortality rates to vary from a low of 0.78 to a high of 0.86. Fishing mortality represents only about 3–18 percent of the total loss.

Causeways in the Prudhoe Bay region do not appear to affect greatly the recruitment rate of young-of-the-year to the Colville River region, mainly because the event is apparently a passive drift process controlled by wind events (Gallaway et al. 1987; Fechhelm and Fissel 1988). The impacts of the causeways would seem to be a direct function of the degree to which the structures modify circulation in a manner that would enhance drop-out of young fish prior to reaching the Colville River (e.g., eddy currents, current reductions, etc.). The main current modification resulting from the existing causeways appears to be displacing the alongshore flows seaward as the waters flow around the shoreline discontinuity, and the enhancement of bottom-water flows toward the shore (marine intrusions). Neither modification would be expected to disrupt the transport of small Arctic cisco, assuming they are mainly associated with the upper part of the water column. Results of the Endicott Monitoring Program (Cannon et al. 1987) appear to confirm this assertion.

Causeways in the Prudhoe Bay region have been observed to create habitat discontinuities such that fish are sometimes prevented from having access to the entire range of feeding habitat. In the worst case, Arctic cisco emanating from the Colville River can lose access to 35 percent of the summer feeding habitat while those associated with the Sagavanirktok River can lose access to 65 percent of the summer habitat (Gallaway et al. 1987). Further, overwintering habitat suitable for Arctic cisco in the Sagavanirktok River appears quite limited. If the habitat discontinuity develops after fish from the Colville have dispersed east of the West Dock causeway, they might become trapped in the area and be forced to attempt to overwinter in the Sagavanirktok River delta. If overcrowding occurred, failure of the overwintering habitat might result.

Results of tagging studies conducted each year during 1981–1986 have shown that fish tagged to the east and west of West Dock return to the Colville River at expected rates (e.g., Craig and Griffiths 1981; Critchlow 1983; Griffiths et al. 1983; Cannon et al. 1987; Fechhelm et al. 1989). These results suggest that, to date, fish from the Colville River isolated in habitats in Prudhoe Bay and eastward during summer have not been trapped there beyond the onset of winter. Successful overwintering of Arctic cisco in the Sagavanirktok River delta is almost certain to have occurred during the period 1981–1985, but at least one pool failed in winter of 1985–1986—apparently due to oxygen depletion (Schmidt et al. 1989). The failure did not appear attributable to an influx of new recruits, but rather to a high density of fish becoming restricted by ice growth to a small pool. The oxygen depletion may also have been augmented if not caused by the sampling activity.

Comparisons of condition or health of fish known or believed to have spent most of the summer period east of West Dock based upon tag return analyses with health or condition of fish which spent most of the summer west of West Dock have not yielded significant differences (Fechhelm et al. 1989). Collectively, these data support an hypothesis that the observed impacts of causeways on fish distribution have had little if any impact on population health.

By contrast, Moulton et al. (1985, 1986) have shown that Arctic cisco some 3 to 7 years in age collected from Prudhoe Bay in 1983 and 1984 were smaller than fish of the same ages from Simpson Lagoon in 1977, from Prudhoe Bay in 1975 and 1976, and from Oliktok Point (west of the Prudhoe Bay area) in 1982 and 1983. Assuming no errors in aging, and that the fish in the Prudhoe Bay samples were resident fish associated with Sagavanirktok River delta overwintering sites, the implication is that the periodic discontinuities in habitat may significantly affect growth of fish restricted in summer to habitats east of the causeway.

Nevertheless, the observed rates of growth of Arctic cisco associated with each of the two habitats appear equivalent (see Moulton et al. 1985). The size difference was set early and has been maintained, but fish from the two areas are growing at equal rates. One plausible ex-

planation for such an event is provided in the recruitment pattern of age-0 and -1 Arctic cisco in 1985. Larger young-of-the-year passed through the Prudhoe Bay region earlier than smaller young-of-the-year fish. Perhaps only smaller fish characteristic of the late migration period took up residence in the Sagavanirktok River delta during the year of recruitment, assuming that the larger fish in the early period of the migration were carried past this area. Furthermore, the small fish that first overwintered in the Sagavanirktok River delta began their second growing season later than Colville fish because the Colville Delta develops open water earlier each spring.

At present, the weight of the evidence supports the contention that no significant population level effects have occurred due to the impacts of the Alaskan fisheries or hydrocarbon developments on anadromous fish habitat. If significant effects do occur in the future, whether they affect the entire population of Arctic cisco or only local populations will ultimately depend on the proportion of the stock subject to these effects. Studies designed to resolve this issue should be of paramount importance.

CONCLUSIONS

The model developed by Gallaway et al. (1983) has yielded blind predictions of catches for 1982–1985 that consistently overestimated actual CPUE but mimicked relative change in actual CPUE in 3 out of 4 years. We believe the model has promise based upon the biological reasonableness of the parameters and the independent observations of year class strengths in recent years. The latter data suggest that the model predictions for the next 5 to 7 years are reasonable. The model would likely be improved if the simple stock–recruitment term in the present model could be supplemented with more mechanistic submodels dealing with the parameters of egg and larval survival, and postlarval (age-0) transport.

We tentatively conclude that present harvest levels and development impacts have not been sufficient to result in measurable effects upon the population on either a regional (total stock) or local scale. For the former premise, it would be necessary to confirm that the average proportion of the total stock that utilizes Alaskan habitats is on the order of 30–40 percent (or less) before the assessment can be readily accepted.

To confirm the presumption that local populations are not being significantly affected by the observed causeway effects on the local environments will require continued monitoring of the distributional response of Arctic cisco to conditions around the existing causeways and the ramifications of these responses as expressed in terms of their health or condition, growth, and their ability to return to the Colville River delta overwintering habitats in late summer and fall.

The stock-origin premise proposed by Gallaway et al. (1983) has not been invalidated. On the contrary, subsequent studies yield additional credence to the hypothesis. Continued genetic studies would go far towards resolving this question, as well as contribute towards resolving the important question—what proportion of the overall population makes use of Alaskan waters?

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